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The Pampas Cat Group (Genus *Lynchailurus* Severtzov, 1858) (Carnivora: Felidae), a Systematic and Biogeographic Review

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ABSTRACT

A systematic study of 86 specimens of South American cats formerly known as *Felis colocolo* reveals three species, in addition to a new subspecies described herein. The three species are grouped in the genus *Lynchailurus* on the basis of shared character states. *Lynchailurus pajeros* occurs on high-elevation steppes from Ecuador to Bolivia and Argentina (eastern slope of the Andes), and farther south in Argentina into lowland steppe, shrubland, and dry forest habitats. Its southern limit is Patagonia (Argentinean and Chilean). *Lynchailurus braccatus* is found in Brazil, Paraguay, and Uruguay, where it occupies humid and warmer grassland and forested areas, at moderate elevations. *Lynchailurus colocolo* occurs in subtrop-

ical forests at middle elevations in central Chile, and in high-elevation steppes in northern Chile on the western slope of the Andes. The latter species may be endangered, because its distribution is limited. Assigned subspecies are as follows: *L. pajeros budini* and *L. p. crespoi*, in northwestern Argentina; *L. p. crucinus*, in southern Argentina and Chile; *L. p. garleppi*, in Peru; *L. p. pajeros*, in central Argentina; *L. p. steinbachi*, in Bolivia; *L. p. thomasi*, from Ecuador; *L. braccatus braccatus*, in southwestern Brazil and Paraguay; *L. b. munoai*, in Uruguay and southern Brazil; *L. colocolo colocolo*, in central Chile; and *L. c. wolffsohni* (new subspecies), in northern Chile.

RESUMEN

Un estudio sistemático realizado sobre una muestra de 86 ejemplares del felido sudamericano anteriormente conocido como *Felis colocolo* revela tres especies, además de una nueva subespecie descrita en este artículo. Estas tres especies se agrupan en el género *Lynchailurus*, utilizando como base estados de carácter compartidos. *Lynchailurus pajeros* se extiende a lo largo de las estepas de altura desde Ecuador hasta Bolivia y Argentina (en la vertiente oriental de los Andes), extendiéndose hasta Argentina, donde desciende a hábitats esteparios y bosques secos a baja altitud, llegando hasta la Patagonia (Argentina y Chile). *Lynchailurus braccatus* se encuentra en Brasil, Paraguay y Uruguay, donde ocupa praderas y bosques más húmedos y cálidos, de altitud moderada. *Lyn-*

chailurus colocolo aparece en bosques subtropicales de altitud media en Chile central, y en estepas de altura en el norte de Chile, en la vertiente occidental de los Andes. Esta última especie podría encontrarse amenazada, ya que habita un área muy limitada. Las subespecies asignadas son las siguientes: *L. pajeros budini* y *L. p. crespoi*, en el Noroeste de Argentina; *L. p. crucinus*, en el sur de Argentina y Chile; *L. p. garleppi*, en Perú; *L. p. pajeros*, en el centro de Argentina; *L. p. steinbachi*, en Bolivia; *L. p. thomasi*, en Ecuador; *L. braccatus braccatus*, en el Suroeste de Brasil y Paraguay; *L. b. munoai*, en Uruguay y sur de Brasil; *L. colocolo colocolo*, en el centro de Chile; y *L. c. wolffsohni* (nueva subespecie), en el norte de Chile.

INTRODUCTION

Felids have engendered considerable systematic controversy, and the pampas cat, usually known as *Felis colocolo*, is no excep-

tion. The cause of the problem is the same as for other cats: small samples, lack of information, ambiguous original descriptions,

and authors ignoring earlier publications. Different generic classifications resulting from the study of a variety of characters (e.g., morphological, morphometrical, behavioral, biochemical, and cytogenetic) have resulted in the recognition of 4 to 19 genera. The tendency during recent years to group many felid species into large cosmopolitan genera (e.g., Ellermann and Morrison-Scott, 1966; Honacki et al., 1982; Corbet and Hill, 1980, 1986, 1991) has simplified the nomenclature, but these assemblages are not supported by original data.

The first published record of the *colocolo* group was provided by Azara (1801), who mentioned a cat from the pampas of Buenos Aires, Argentina, the "chat pampa" ("pajero" in his Spanish version, published in 1802). Three species related to the "chat pampa" or "pajero" have been described to date: *Felis colocolo* Molina, 1782; *Felis pajeros* Desmarest, 1816; and *Felis braccata* Cope, 1889; along with several subspecies of each. Nomenclatural problems related to *colocolo* started when Hamilton Smith (in Griffith et al., 1827) published a drawing of a specimen collected in Guyana, which he identified as Molina's *colocolo*. Although the external characters illustrated are not now considered to be diagnostic, many authors (e.g., Gay, 1847; Mivart, 1881) followed Hamilton Smith's identification. Other researchers seemed to ignore Gray's (1874) criticism of this drawing. The true identity of *colocolo* became even more confused when Philippi (1869) associated *colocolo* with the Andean mountain cat, *Oreailurus jacobitus* (Cornalia, 1865), an opinion accepted by many authors. Pocock (1941) even proposed the generic name *Colocolo* for the Andean mountain cat. Cabrera (1940), however, showed that Molina's *colocolo* and Cornalia's *jacobitus* were different animals. He also called attention to the affinity between all populations assigned to *colocolo*, *braccata*, and *pajeros* (the latter two names were placed in the synonymy of *pajeros* by Allen, 1919), and proposed including them all under *Lynxchailurus colocolus*. Pocock (1941) included the same forms under *pajeros* because he believed (as did Allen) that *colocolo* and *jacobitus* were synonyms. Obviously, Pocock had

not seen Cabrera's (1940) paper, which was published close to the same time. *Felis colocolo* has since been regarded as a polytypic species.

I found some unusual patterns of variation within the populations identified as *colocolo* while conducting a phylogenetic study on the living species of felids. An examination of all available museum specimens reveals that this assemblage consists of three closely related species. Their diagnostic characters and geographic distributions are the subject of this report.

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MATERIALS AND METHODS

Suitable samples of felids are usually difficult to obtain. Often only skins without skulls are available and many specimens are juveniles. Specimens of Pampas cats are also scarce in collections. For this study, I examined 86 specimens, consisting of 72 study skins and 51 skulls, from eight large North American, South American, and European collections (see Appendix 1). The original sample consisted of 102 specimens, but 16 were subsequently excluded because they came from zoos, had unknown localities, or had been misidentified (Appendix 2).

The collections consulted or mentioned in the text, with their acronyms (after Duellman et al., 1978) are the following:

AMNH	American Museum of Natural History, New York (USA)
BM	Natural History Museum, London (United Kingdom)
EBD	Estación Biológica de Doñana, Sevilla (Spain)
FMNH	Field Museum of Natural History, Chicago (USA)
KU	University of Kansas, Museum of Natural History, Lawrence (USA)
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires (Argentina)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge (USA)
MHNM	Museo de Historia Natural de Montevideo, Montevideo (Uruguay)
MLP	Museo de La Plata, La Plata (Argentina)
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley (USA)
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor (USA)
USNM	National Museum of Natural History, Washington D.C. (USA)
ZMB	Zoologisches Museum, Berlin (Germany)

Adults are specimens having the sphenoccipital synchondrosis totally ossified, as previously observed on lynxes (Garcia-Perea, 1991). My observations on several felid species indicate that this is a valid criterion for determining skeletal maturity.

I began my evaluation of morphological variation using 175 qualitative characters of the cranium, mandible, and teeth, developed for comparisons among living species of felids worldwide. However, only 12 characters presented useful variation in my sample of the colocolo group, and these are described in this paper, using the terminology of Jayne (1898), Gaunt (1959), and Hunt (1974, 1987).

Data for five external measurements (in millimeters and grams) were taken from information on specimen labels. I used digital calipers to take 10 cranial measurements (recorded to the nearest 0.01 mm). Only adults were measured for this study. Measured variables, commonly used for felids, and their abbreviations, are as follows (fig. 1):

HB	Head + body length. Tip of nose to dorsal base of tail.
T	Tail length. Dorsal base to tip of tail (not including hairs).
HF	Hind foot length. Distal tip of pad of longest toe, to edge of heel.
E	Ear length. Maximum length from inferior notch to tip of pinna.
W	Weight (mass).
GLS	Greatest length of skull along the medial plane.
CBL	Condylbasal length. Distance from anterior margin of incisive alveoli to posteriormost surface of occipital condyles.
RWC	Rostral width across canines. Maximum width across outer margins of upper canines.
MW	Mastoid width. Maximum breadth across mastoid processes.
IOW	Interorbital width. Least distance between orbits.
POW	Postorbital width. Least distance across postorbital constriction.
ZW	Zygomatic width. Maximum distance across zygomatic arches.
P4L	Length of P4 at cingulum. Greatest length, on labial side, on cingulum.
ML	Mandible length. Length of mandible from anterior margins of incisive alveoli to posterior surface of condylar process.

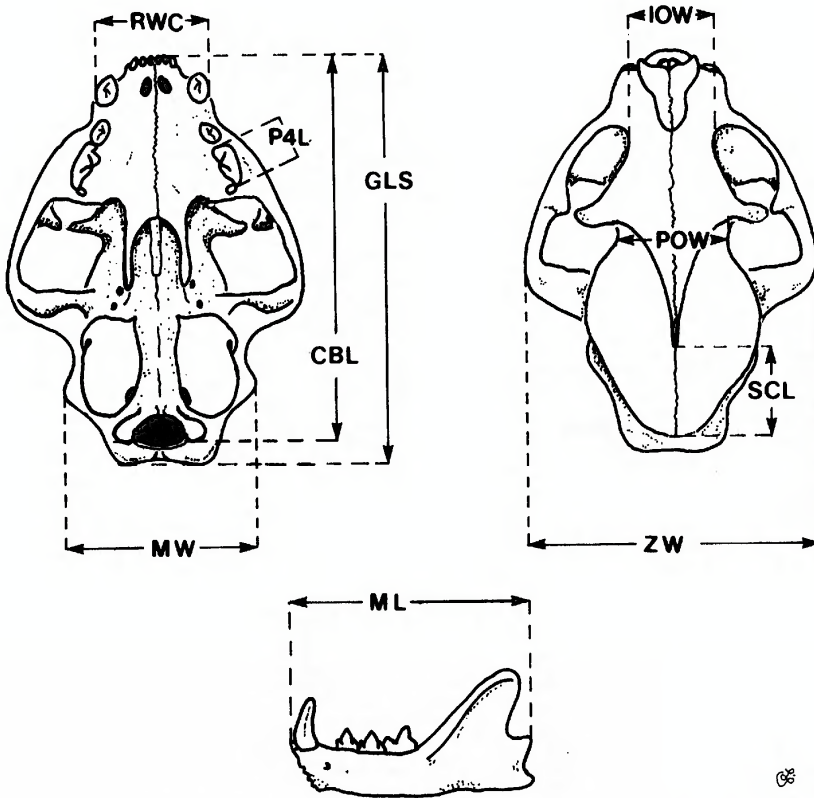


Fig. 1. Variables measured from skulls examined or from the literature.

Variables medidas en cráneos examinados o tomadas de la bibliografía.

GLS	Greatest length of skull (Longitud total craneal)
CBL	Condylobasal length (Longitud condilobasal)
RWC	Rostral width across canines (Anchura rostral a nivel de los caninos)
MW	Mastoid width (Anchura mastoidea)
IOW	Interorbital width (Anchura interorbitaria)
POW	Postorbital width (Anchura de la constricción postorbitaria)
ZW	Zygomatic width (Anchura zigomática)
P4L	Length of P4 at cingulum (Longitud del P4 en el cíngulo)
ML	Mandible length (Longitud mandibular)
SCL	Length of sagittal crest (Longitud de la cresta sagital)

SCL	Length of sagittal crest. Maximum length of sagittal crest.
SCL/GLS	Ratio representing length of sagittal crest relative to greatest length of skull.

My descriptions of pelage variation emphasize the characteristics and distribution of the markings. Spotting patterns are important in felid systematics. Closely related cats sometimes show similar patterns, which are misinterpreted (e.g., *Lynx lynx* has been confused with *Lynx pardinus* in Carpathian and Caucasus Mts.). Color is also important, but is unreliable in old study skins because

of fading. Many earlier publications contain carefully detailed color descriptions made on fresh or recently collected specimens (for *colocolo* see Azara, 1802; Cope, 1889; Wolffsohn, 1908; Lönnberg, 1913; Pocock, 1941; Cabrera, 1961; Ximenez, 1961).

For convenience, I recognized five units for the morphological analysis (fig. 2). Each represents an apparently continuous population.

GAZETTEER

I used primary data from specimen labels and the collector's fieldnotes to develop this

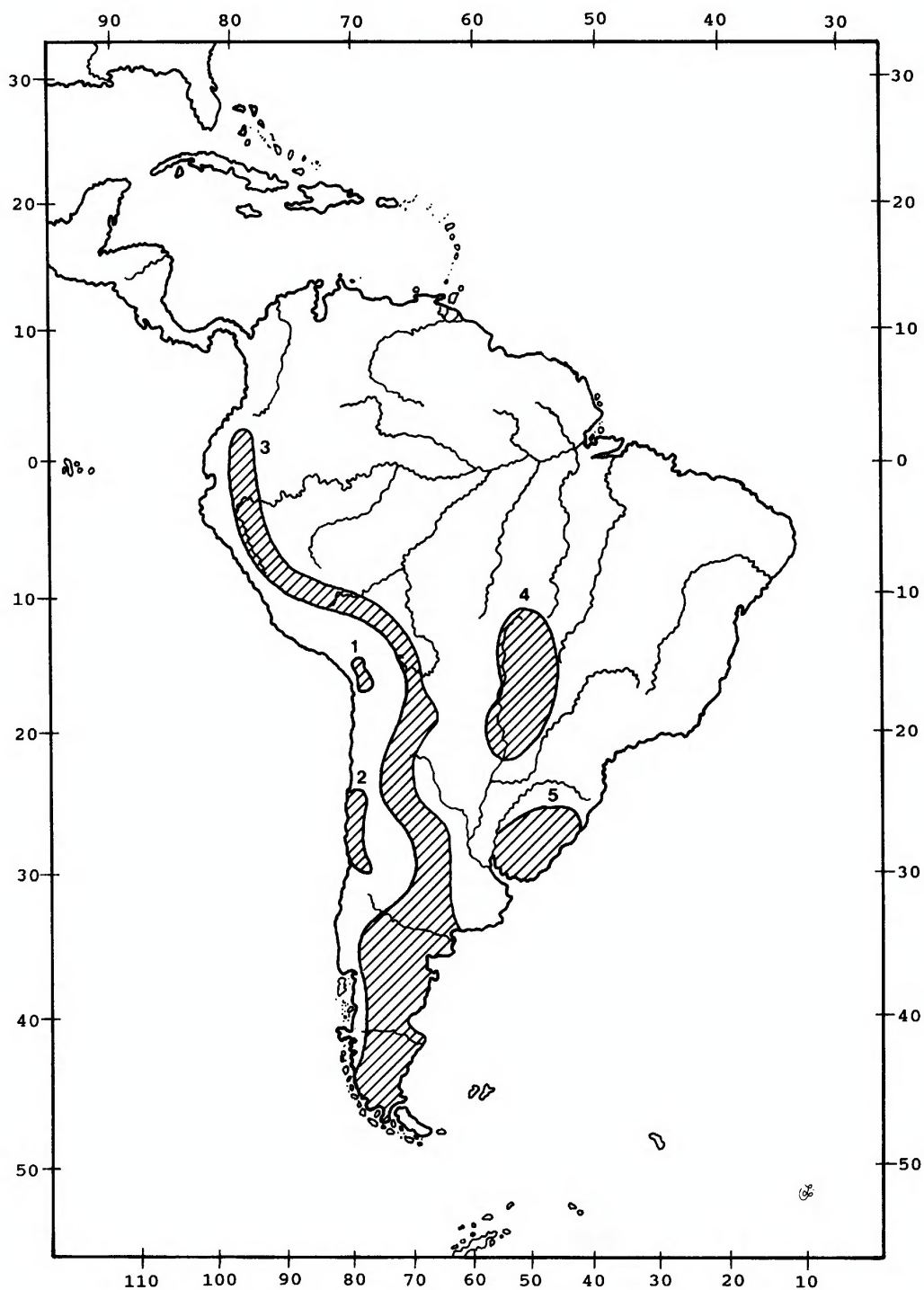


Fig. 2. Distribution of *Lynchailurus colocolo*, showing the five populations considered for morphological analysis.

Distribución de *Lynchailurus colocolo*, mostrando las cinco poblaciones consideradas para el análisis morfológico.

gazetteer. Other data were obtained from the Ornithological Gazetteers published by the Museum of Comparative Zoology at Harvard, from the gazetteers published by the US Board on Geographic Names, and from the Times Atlas of the World (1990, 8th ed.). Additional information from the taxonomic literature is indicated in parentheses immediately after the record.

Information includes: names of localities arranged by political divisions (provincia, departamento, estado) within each country; elevation above sea level in meters; and geographic coordinates (latitude south / longitude west). Elevations in parentheses were taken from reference sources and often represent the elevational range of a mountain or elevations determined from topographic lines on maps. Elevations without parentheses are original data from collectors. Localities are plotted in figure 3.

ARGENTINA

Provincia Buenos Aires:

1. 20 mi S San Blas (sea level), 40°33'S/62°15'W.
2. Estancia San José (sea level), 40°08'S/62°55'W.

Provincia Catamarca:

3. La Atravesada, Dpto. Andalgalá, 1800 m, 24°22'S/64°20'W.
4. Antofagasta de la Sierra (3450 m), 26°04'S/67°25'W.
5. Catamarca (501 m), 28°28'S/65°47'W.

Provincia Córdoba:

6. Salinas de Serrezuela (279 m), 30°38'S/65°23'W.

Provincia Chubut:

7. Río Senguerr (200–500 m), 45°32'S/68°54'W.

Provincia Jujuy:

8. Sierra de Santa Victoria (3000–5000 m), 22°23'S/65°17'W.

Provincia La Pampa:

9. Estancia El Retoño, General San Martín (150 m), 38°18'S/63°39'W.
 10. Victorica (311 m), 36°13'S/65°27'W.
 11. Telén (302 m), 36°16'S/65°30'W.
 12. Departamento Caleu-Caleu (100–200 m), 38°35'S/64°00'W.
 13. Toay (190 m), 36°40'S/64°21'W.
 14. Puelches (200 m), 38°09'S/65°55'W.
- Provincia La Rioja:
15. Sierra Velazco (1000–4000 m), 29°05'S/67°05'W.
 16. Villa Unión (1240 m), 29°18'S/68°12'W.
- Provincia Neuquén:
17. Between Catán-Lil and Las Coloradas (1000 m), 39°39'S/70°36'W.

18. Collón-Curá (1000–2000 m), 40°07'S/70°44'W.

Provincia Río Negro:

19. Estancia Huanu-luan (950 m), 41°22'S/69°52'W.
20. Viedma (40 m), 40°48'S/63°00'W.
21. Maquinchao (888 m), 41°15'S/68°44'W.
22. Southern border of Nahuel Huapi lake (767 m), 40°58'S/71°30'W.
23. Ministro Ramos Mexía (502 m), 40°30'S/67°17'W.

Provincia Salta:

24. Chorrillos Mt., 5000 m, 24°11'S/66°21'W.
25. Aguaray (565 m), 22°16'S/63°44'W.

Provincia Santa Cruz:

26. Río Gallegos (sea level), 51°38'S/69°13'W.
27. Cabo Tres Puntas (sea level), 47°06'S/65°33'W.

Provincia Tucumán:

28. Concepción (400 m), 27°20'S/65°35'W.

BOLIVIA

Departamento Cochabamba:

29. Tiraque, 4000 m, 17°25'S/65°43'W.

BRAZIL

Estado Mato Grosso:

30. Descalvado (142 m), 16°45'S/57°42'W.
31. Chapada dos Guimarães (793 m), 15°26'S/55°45'W.

Estado Mato Grosso do Sul:

32. Maracajú (500–1000 m), 21°38'S/55°10'W.
33. Fazenda Piquí, Aquidauana (160 m), 20°28'S/55°48'W (Ximenez, 1970).

Estado Rio Grande do Sul:

34. São Lourenço do Sul (sea level), 31°22'S/51°58'W (Ihering, 1911).

CHILE

Provincia Aconcagua:

35. Mountains above Catapilco lake (900 m), 32°34'S/71°17'W.

Provincia Coquimbo:

36. Marquesa (337 m), 29°58'S/71°00'W (Osgood, 1943).

Provincia Magallanes:

37. Puerto Prat, Ultima Esperanza Inlet (100 m), 51°38'S/72°38'W.
38. Cerro Castillo (1110 m), 51°16'S/72°21'W (Johnson et al., 1990).

Provincia Santiago:

39. Santiago (500 m), 33°27'S/70°40'W.
40. Vegas de Curacaví (100 m), 33°24'S/71°09'W.

Provincia Tarapacá:

41. Camarones river (2000–4000 m), 19°01'S/69°52'W (Mann, 1945).
42. Putre, Tacna, 4120 m, 18°12'S/69°35'W.

Provincia Valparaíso:

43. Malacará (300 m), 33°00'S/71°05'W.

44. Cerro Llai-Llai, 800 m, 32°50'S/70°57'W.
45. Limache (85 m), 33°00'S/71°16'W.
46. Cerro de la Campana, Quillota, 1800 m, 32°57'S/71°08'W.
47. Punta Caraumilla (sea level), 33°06'S/71°44'W.
48. Viña del Mar (sea level), 33°02'S/71°35'W (Wolffsohn, 1908).

ECUADOR

Provincia Napo:

49. Cerro Antisana, E side (5704 m), 00°30'S/78°08'W.

Provincia Pichincha:

50. Quito (2818 m), 00°13'S/78°30'W.
51. Cerro Pichincha, NE side, 3660 m, 00°10'S/78°33'W.

PARAGUAY

Departamento Presidente Hayes:

52. Fortín Juan de Zalazar (150 m), 23°06'S/59°18'W.

Departamento Central:

53. Asunción (77 m), 25°15'S/57°40'W.

Departamento Concepción:

54. San Luis de la Sierra (200 m), 22°25'S/57°27'W (Weigel, 1961).

PERU

Departamento Amazonas:

55. Condechaca, Rio Utcubamba, 2134 m, 05°30'S/78°32'W.

Departamento Cuzco:

56. Hacienda Capana, near Ocongate (3500–4000 m), 13°28'S/71°25'W.

Departamento Huánuco:

57. Ambo (2064 m), 10°05'S/76°07'W.

Departamento Pasco:

58. Huariaca, 2745 m, 10°27'S/76°07'W.

Departamento Puno:

59. Picotani (4390 m), 14°33'S/69°48'W.
60. Ilave, 3962 m, 16°05'S/69°40'W.
61. Putina, 3962 m, 14°55'S/69°52'W.

URUGUAY

Departamento Cerro Largo:

62. Tarariras (100–200 m), 32°28'S/55°01'W (Ximenez, 1961).

Departamento Lavalleja:

63. Zapicán (231 m), 33°31'S/54°55'W (Ximenez, 1961).

Departamento San José:

64. Hacienda Herminia, Parque San Gregorio (0–100 m), 34°41'S/56°50'W.
65. Chamizo (0–100 m), 34°15'S/55°56'W (Ximenez, 1961).

Departamento Soriano:

66. Arroyo Perdido (0–100 m), 33°23'S/57°22'W (Ximenez, 1961).

MORPHOLOGICAL VARIATION IN SKULLS

BULLAR REGION

The auditory bulla of felids is formed by three elements (ectotympanic, rostral entotympanic, and caudal entotympanic), and consists of two chambers separated by a septum (Hunt, 1974, 1987). The anterior chamber is formed by the rostral entotympanic (poorly developed in felids) and the ectotympanic (T); the posterior, by the caudal entotympanic (CE; fig. 4). The position of the septum (S) is marked by an obvious groove in the ventral side of the bulla that extends diagonally from its anterointernal corner to the midpart of the lateral wall, behind the auditory meatus. The anterior chamber is approximately ring-shaped; the posterior, navicular-shaped. The degree of development of both chambers is variable between species, but the relative size of ectotympanic in relation to caudal entotympanic usually is consistent within species. Some variation in the degree of inflation of the posterior chamber may be evident between subspecies. I recognize three types of variation in the relative size of ectotympanic and entotympanic, as described below.

Ectotympanic. This bone shows variation in the degree of development of its posteroventral region. To evaluate this feature, I estimated the percentage of total bullar volume represented by the ectotympanic. The three types found (fig. 4) are:

Type 1—Has the largest ectotympanic (40–50% of bullar volume), which is inflated ventrally and posteriorly. All specimens of populations 1 and 2 belong to this type, along with a single specimen from population 3 (USNM 172786). The ectotympanic is slightly smaller in population 1 than in population 2, a difference estimated to be about 10% of bullar volume.

Type 2—Has a moderately developed ectotympanic (25–35%), which is expanded ventrally and posteriorly, but not so conspicuously inflated as in the previous group. This type characterizes specimens of population 3, with the single exception noted earlier. I found some geographic variation in this character. Specimens in the northern half of

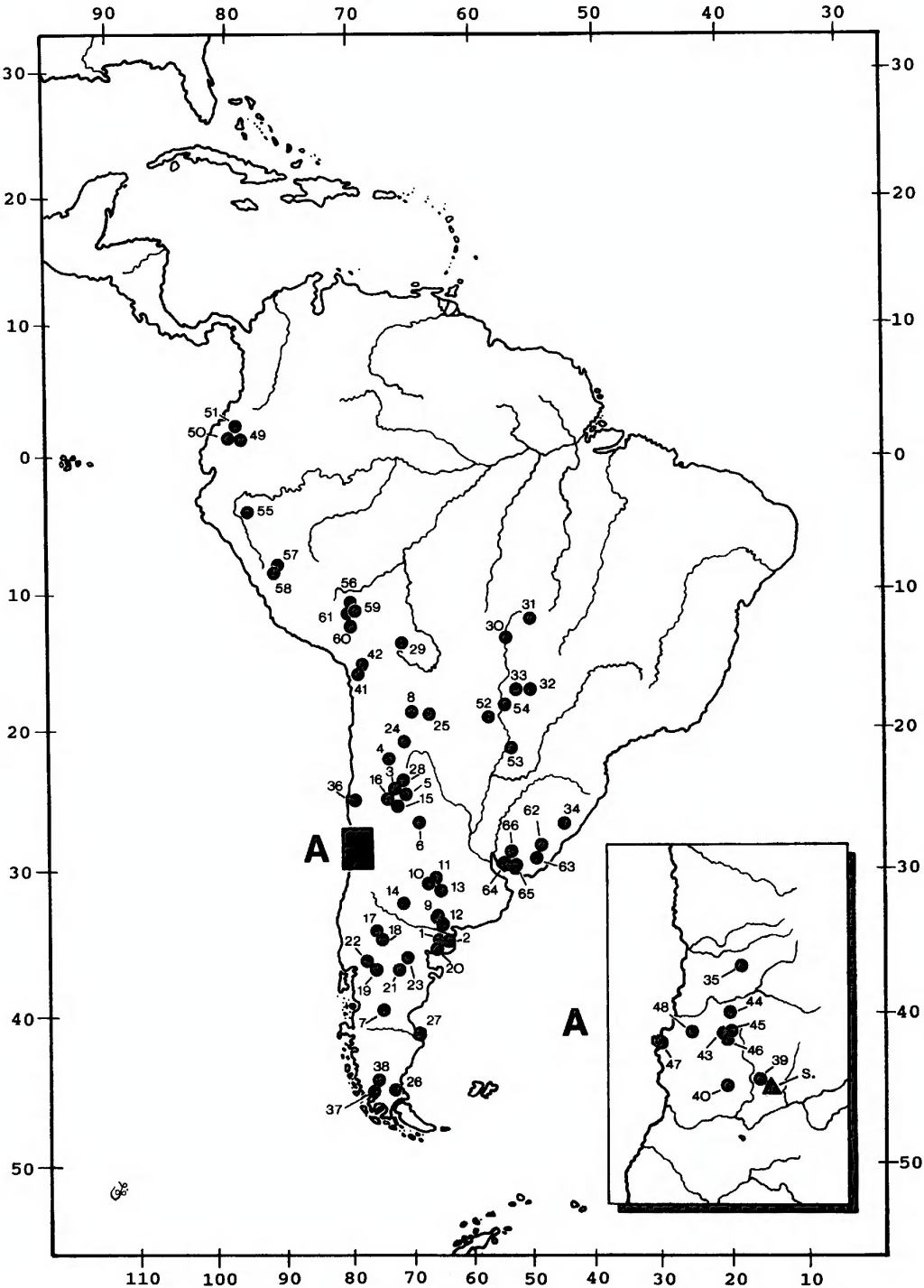


Fig. 3. Localities where specimens have been collected. Names corresponding to the numbers are in the gazetteer. Area in black square has been enlarged (A). Black triangle (S.) is Santiago, Chile.

Localidades donde se colectaron los ejemplares. Los nombres correspondientes a los números están en el "gazetteer." El área incluida en el cuadrado negro ha sido aumentada (A). El triángulo negro (S.) es Santiago, Chile.

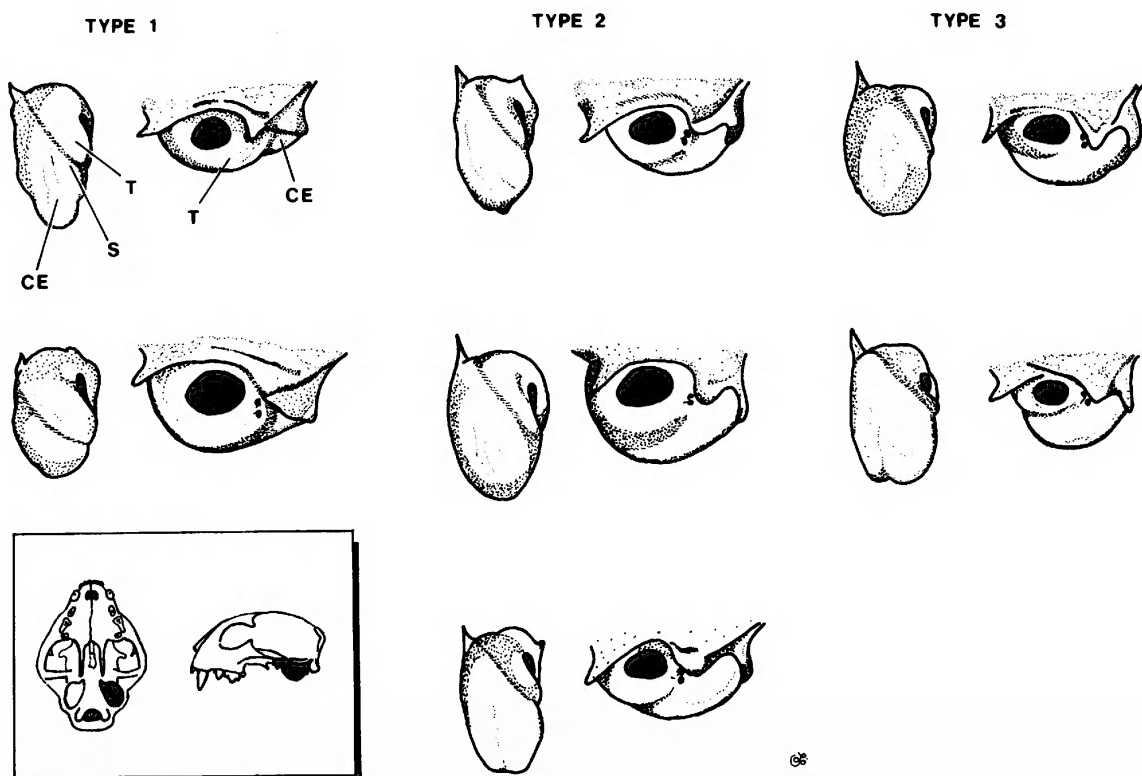


Fig. 4. Three types of bulla in relation to the degree of development of ectotympanic (T) and caudal entotympanic (CE), in ventral (left) and lateral (right) view. (S) septum groove.

Tres tipos de bulla en relación con el grado de desarrollo del ectotimpánico (T) y entotimpánico caudal (CE), en normas ventral (izquierda) y lateral (derecha). (S) surco del septum.

the range show 25–30% of bullar volume; those in the southern half, 30–35%.

Type 3—Lack significant posteroventral expansion or inflation of the ectotympanic, which represents 20–25% of bullar volume. Specimens from populations 4 and 5 show this type of bulla.

Variation in inflation of the bullae, reported for these cats by Allen (1919) and Pocock (1941), agrees with my results. Allen (1919) compared two specimens representing my populations 5 and 3, respectively, and said that the bulla was less inflated in the former than in the latter. Pocock (1941) recorded a relatively larger anterior chamber in the bullae of specimens representing my populations 2 and 3 (southern part) than was found in specimens from other areas.

Caudal entotympanic. Variation in this part of the bulla is related to the degree of ectotympanic development. Large ectotympanics are associated with small caudal entotym-

panics. Correlated with the three types of ectotympanic development just described, I found poorly developed entotympanics in specimens of type 1. In lateral view (fig. 4) the ectotympanic extends below the ventral limit of the entotympanic. Specimens of type 3 present the opposite extreme, with the caudal entotympanic well-developed anteriorly, its ventral portion remarkably inflated. In lateral view, the entotympanic of type 3 specimens exceeds the ventral limit of the ectotympanic. Specimens of type 2 show an intermediate morphology, but the entotympanic still extends below the ectotympanic in lateral view.

Morphology of mastoid processes. These processes are located over the posterodorsal part of the bulla, and the extent of their contact with bullae is variable and correlated with development of the mastoid process. I found two morphotypes for this character (fig. 5):

Type 1—Mastoid process (MP) poorly de-

veloped posteriorly and separated from the paroccipital process (PP) by a wide notch revealing the surface of the bulla between them. Mastoid and paroccipital processes are only in contact dorsally (fig. 5A). With slight variations, this morphotype appears in populations 3, 4, and 5. In specimens of population 3, the paroccipital processes tend to be short and projected slightly backwards. In populations 4 and 5, these processes tend to be longer, cup-shaped, and cover the bulla posteriorly.

Type 2— Mastoid process well developed posteriorly, and covers the bulla (fig. 5B). This condition is typical of population 2. Specimens of population 1 show an intermediate condition in which part of the bullar surface is exposed laterally.

ORBITAL REGION

Inferior oblique muscle fossa. This fossa (IOMF), origin of inferior oblique muscle, occupies one of two different positions in the orbital wall:

Type 1— Fossa located on the lacrimal-palatine-maxilla suture (fig. 6A). All populations except 1 and 2 show this type.

Type 2— Fossa situated on the lacrimal-palatine suture (fig. 6B). All specimens from populations 1 and 2 show this type.

PALATAL REGION

Shape of notch for postpalatine vein. The shape of this notch, usually consistent within felid species, showed some individual variation, but in general, two morphotypes can be distinguished:

Type 1— Notch for postpalatine vein wide and comparatively shallow (fig. 7A). This morphotype is present in all the specimens from populations 1, 2, and 3.

Type 2— Notch narrow and deep (fig. 7B). This morphotype is typical of populations 4 and 5.

Shape of posterior margin of the palate. I found two morphotypes for the posterior margin of the palate in my sample:

Type 1— U shaped edge, with a medial notch (fig. 8A). This type appears in all the specimens of populations 3, 4, and 5. In populations 1 and 2, only 30% show this type (n = 13).

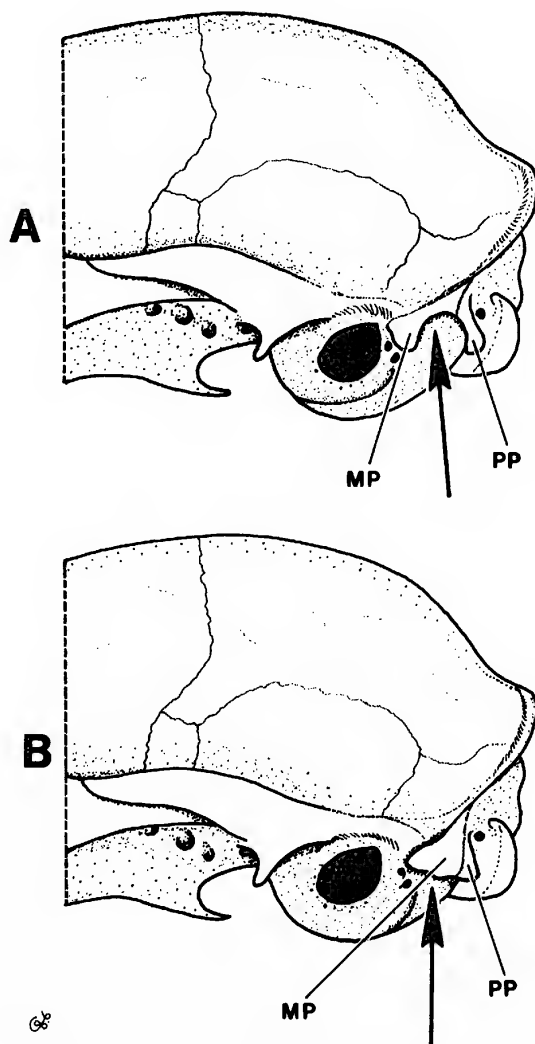


Fig. 5. Lateral view of neurocranium, showing the two types of mastoid processes (MP) in relation to paroccipital processes (PP). (A) type 1; (B) type 2.

Aspecto lateral del neurocráneo, mostrando los dos tipos de procesos mastoideos (MP) en relación con los procesos paraoccipitales (PP). (A) tipo 1; (B) tipo 2.

Type 2— U shaped edge, with no medial notch (fig. 8B). This type appears in 70% of specimens from populations 1 and 2.

NEUROCRANIUM

Development of the sagittal crest. In juvenile animals, there is no sagittal crest; instead a pair of temporal ridges (TL) runs along the parietals, nearly paralleling the suture be-

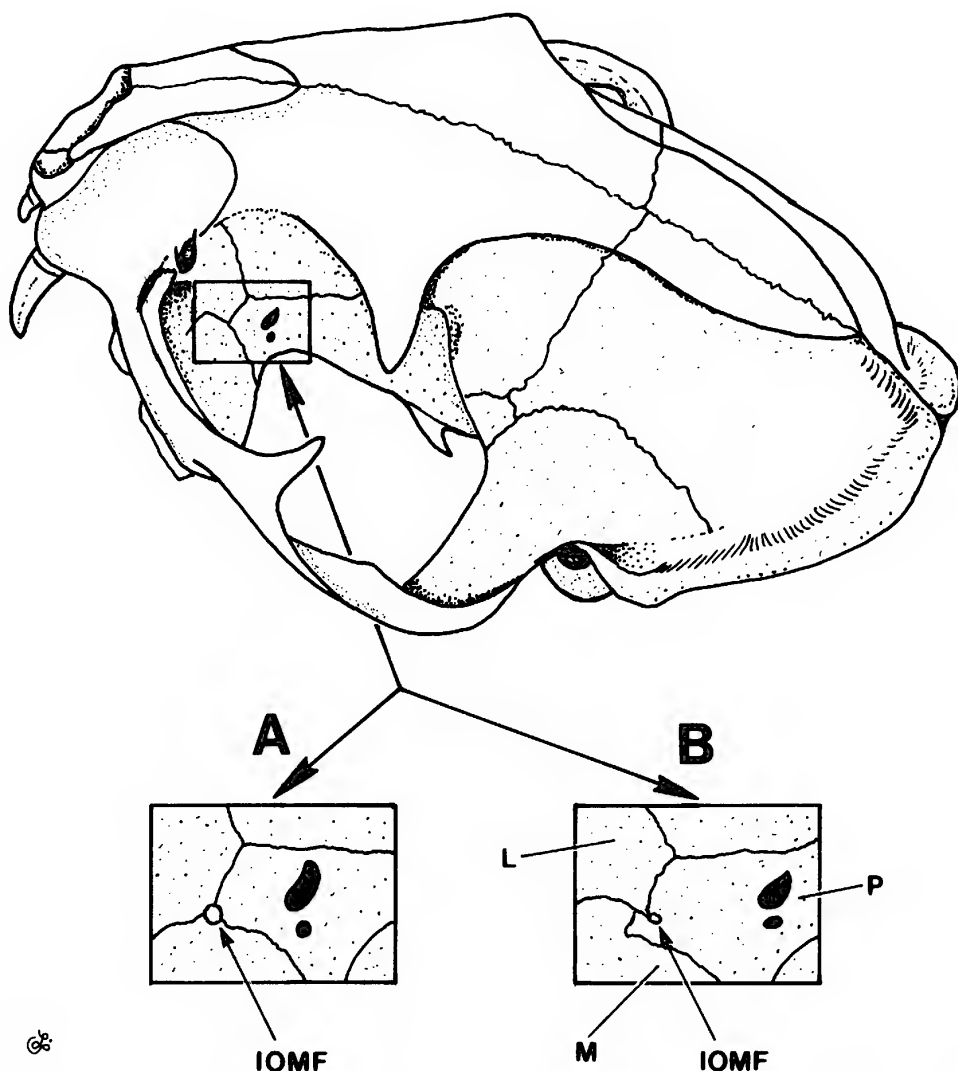


Fig. 6. Two different positions adopted by inferior oblique muscle fossa (IOMF). (A) type 1; (B) type 2. (L) lacrimal bone; (M) maxilla bone; (P) palatine bone.

Dos posiciones diferentes adoptadas por la fosa del músculo oblicuo inferior (IOMF). (A) tipo 1; (B) tipo 2. (L) hueso lacrimal; (M) hueso maxilar; (P) hueso palatino.

tween parietals (fig. 9A). During postnatal development, these temporal ridges move closer, and eventually meet on the interparietal (IB) at the midline of the skull. The sagittal crest (SC) starts to develop from that intersect and the lambdoidal crest. With age, the crest lengthens anteriorly, the lyre-shaped area between temporal ridges becoming reduced in length and breadth. Although development of the sagittal crest shows some individual variability, differences also exist between populations. To facilitate analysis, I sorted

all possible levels of development of this structure into four stages as follows (fig. 9):

Type A— Juvenile stage. Temporal ridges present, but no sagittal crest.

Type B— Sagittal crest poorly developed, restricted to interparietal region.

Type C— Sagittal crest moderately developed, occupying posterior half of suture between parietals.

Type D— Sagittal crest well developed, occupying total length of parietal suture.

To avoid ontogenetic variation, I scored

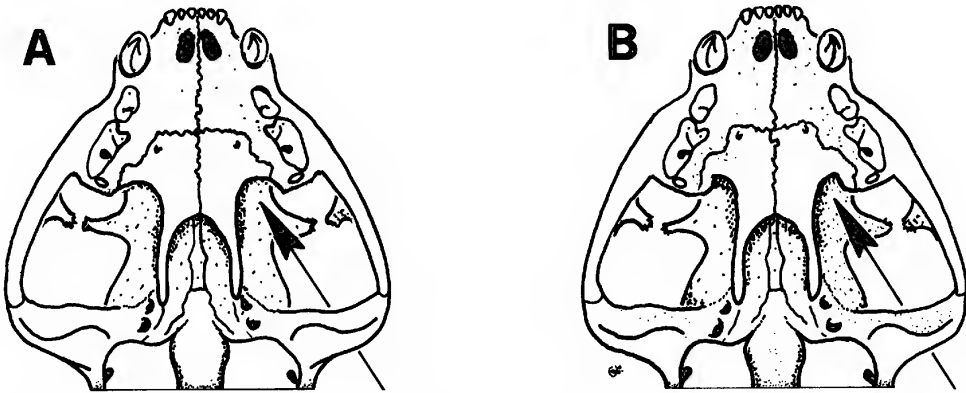


Fig. 7. Two different shapes observed for the notch for postpalatine vein. (A) type 1; (B) type 2.
 Dos formas diferentes observadas en la escotadura para la vena postpalatina. (A) tipo 1; (B) tipo 2.

only adults for this character. All but seven adults from populations 3, 4, and 5 ($n = 23$) show sagittal crest type B. The seven exceptions (30%) show type C. The only adult specimen examined of population 1 fits type C. All specimens of population 2 ($n = 6$) show type D.

TEETH

Frequency of P2. Pampas cats have a tendency to lose the upper second premolar (P2). The tooth appears only occasionally and is poorly developed (fig. 10). Its frequency varies among populations as follows:

Populations 4 and 5. P2 present in com-

paratively high frequency; 63% of the total ($n = 8$).

Populations 1 and 2. Present in a low percentage of individuals, 33% of the total ($n = 6$).

Population 3. Absent in all specimens examined ($n = 21$).

Shape of P3 main cusp. The main cusp (paracone) of the upper third premolar (P3) shows variation in height and shape, as follows:

Type 1 — Paracone narrow and long in lateral view (labial aspect), giving the tooth an acutely pointed appearance (fig. 11, left). This type occurs in all specimens of populations

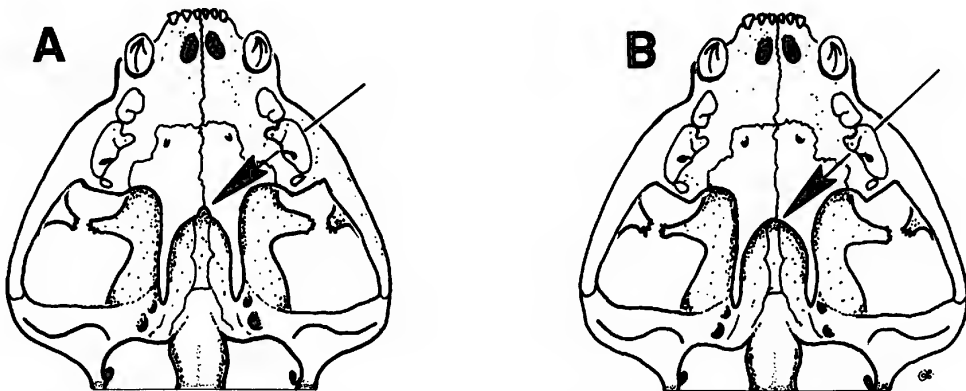


Fig. 8. The two morphotypes observed for the shape of posterior edge of the palate. (A) type 1; (B) type 2.

Los dos morfotipos observados para la forma del borde posterior del paladar. (A) tipo 1; (B) tipo 2.

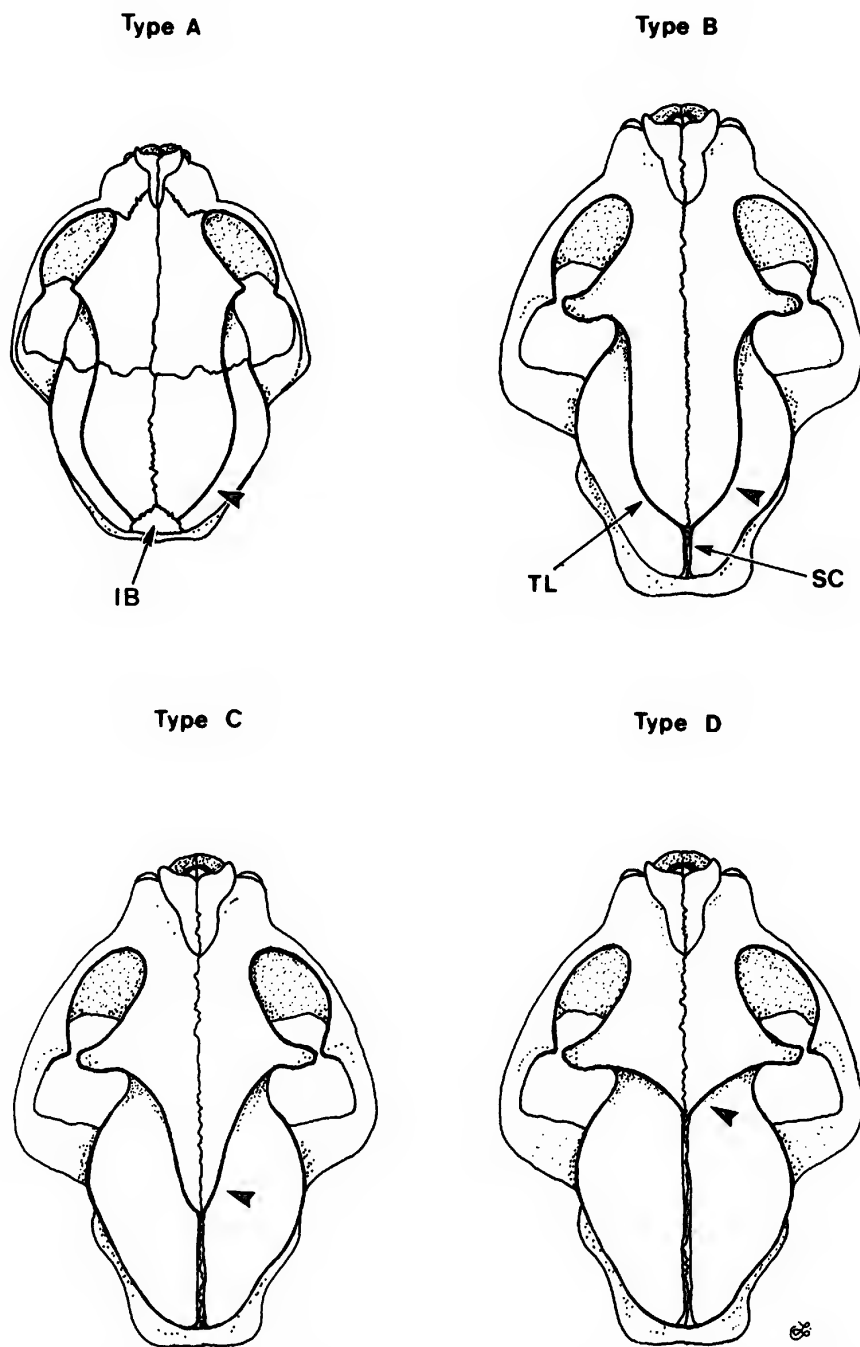


Fig. 9. Different degrees of development of temporal lines (TL) and sagittal crest (SC). Type A, juvenile stage. Types B, C, D, variability among adults. IB: interparietal bone.

Diferentes grados de desarrollo de las líneas temporales (TL) y la cresta sagital (SC). Tipo A, estado juvenil. Tipos B, C, D, variabilidad entre adultos. IB: hueso interparietal.

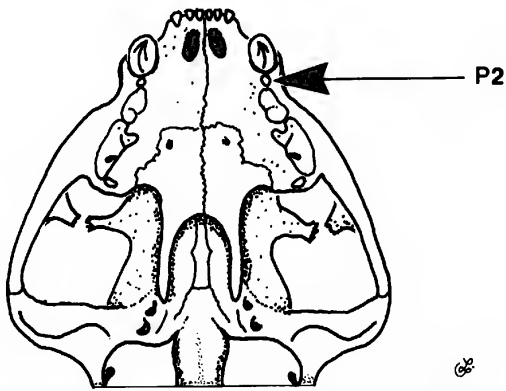


Fig. 10. Size and shape of upper second premolar (P2), as it appears in individuals examined.

Tamaño y forma del segundo premolar superior (P2), según se ha observado en los individuos examinados.

1, 2, and 3, with the exception of specimens from Ecuador.

Type 2— The paracone is short and wide in lateral aspect, lacking the sharp appearance of type 1 (fig. 11 right). This type is present in all specimens of populations 4 and 5, and specimens from Ecuador.

Presence of parastyle on P3. The upper third premolar may have two or three cusps in felids: a main central cusp (paracone), a posterior cusp (metastyle), and sometimes an anterior cusp (parastyle). The parastyle tends to be absent in felids, except in big cats (Salles, 1992). I found this cusp present (although reduced) in three specimens representing populations 4 and 5 (fig. 12 left).

Presence and size of P4 protocone. The upper carnassial (P4) usually has four cusps: two small anterior cusps (parastyle and proto-

cone), a large paracone, and a posterior metastyle (fig. 13). The protocone, which tends to be smaller than the parastyle in felids, is variable in size in the pampas cat group, being absent or vestigial in some specimens (fig. 13 left), but appearing moderately developed in most (fig. 13 right). The protocone is present in 75% of specimens in populations 1 and 2 ($n = 12$), 80% in populations 4 and 5 ($n = 5$), and 83% in population 3 ($n = 23$).

Lingual tubercles on c1. Azara (1802) mentioned the presence of a second cusp on the lower canine, near the incisors (that is, on the lingual side of the tooth) in his Pampean specimens. Ximenez (1961, 1970) mentioned a small protuberance in the same location in specimens from Brazil and Uruguay (populations 4 and 5). I found that all specimens have a protuberance on this part of the canine that represents an enlargement of the basal portion of a ridge running down the lingual surface of the crown (fig. 14A). This protuberance acquires the shape of a small cuspid in some specimens of populations 4 and 5 (fig. 14B). Although I have not seen this cuspid in specimens of populations 1, 2, and 3, the specimen described by Azara belonged to population 3, so it might be possible to find this character in other populations as well.

METRIC CHARACTERISTICS OF SKULLS

Tables 1 and 2 show the values for 14 dimensions and 1 ratio based on measurements on adult specimens from my sample, and on other data collected from the literature (Lönnerberg, 1913; Wolffsohn, 1923; Cabrera, 1961; Ximenez, 1961). Sample sizes of the

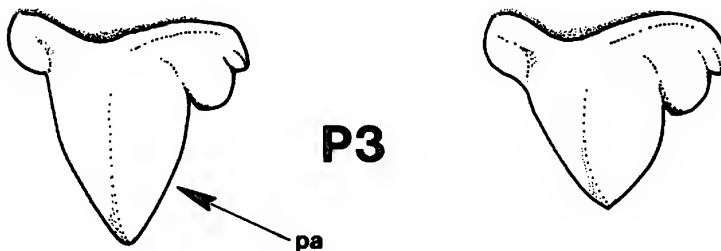


Fig. 11. Shape of upper third premolar (P3) main cusp, paracone (pa). Left, type 1; right, type 2. Forma de la cúspide principal, paracono (pa), del tercer premolar superior (P3). Izquierda, tipo 1; derecha, tipo 2.

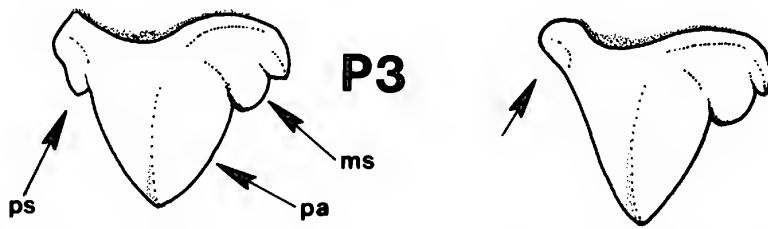


Fig. 12. Parastyle (ps) of upper third premolar (P3) occurs in some specimens (left, type 1), but is absent in others (right, type 2). (pa) paracone; (ms) metastyle.

El parastilo (ps) del tercer premolar superior (P3) aparece en algunos ejemplares (izquierda, tipo 1), pero está ausente en otros (derecha, tipo 2). (pa) paracono; (ms) metastilo.

different populations studied are too small to be useful for statistical analyses, but the values in tables 1 and 2 illustrate some trends in mensural variation.

As in other cats (e.g., lynxes; Garcia-Perea, 1991), there is sexual dimorphism in size within every population, males being larger than females. Cranial measurements of adults also suggest size differences between some populations as follows: (a) specimens of populations 1 and 2 are largest and have the most developed sagittal crests (usually extending full length of parietal suture); (b) specimens of population 3 vary geographically in size, those in the north (Ecuador) being the smallest, and those in Patagonia being largest (similar to those in populations 1 and 2, fig. 2); (c) specimens of populations 4 and 5 are of

medium size and show a little geographical variation from north to south, with the largest in the south (Uruguay).

COAT PATTERN VARIATION

Felids show great variation of coat patterns. Similarity between species has often been used to indicate phylogenetic relationships, and variation within species as taxonomic criteria for subspecific differentiation.

My study of the distribution and characteristics of pelage markings revealed a significant amount of variation, which partially explains the large number of taxa described for this group.

Color and pattern variation for the parts of the head, body, and tail, are as follows:

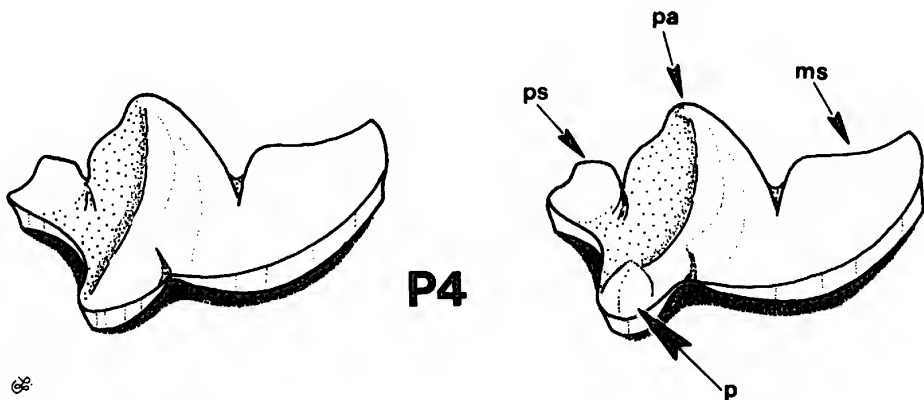


Fig. 13. Protocone (p) of upper fourth premolar (P4) tends to be present in most specimens (right, type 2), but it is absent in a low percentage of them (left, type 1). (ps) parastyle; (pa) paracone; (ms) metastyle.

El protocono del cuarto premolar superior (P4) tiende a estar presente en la mayoría de los ejemplares (derecha, tipo 2), pero está ausente en un pequeño porcentaje de ellos (izquierda, tipo 1). (ps) parastilo; (pa) paracono; (ms) metastilo.

Face: No characteristic pattern, except for two transverse dark lines crossing each cheek, the upper one starting in the external corner of the eye, and the inferior one, almost parallel, running up around the lateral side of the cheeks.

Ears: Usually darker dorsally than surrounding areas, a dark anteroexternal border, and sometimes with a pale spot.

Spinal crest: An erectile crest of fur (about 3 cm wide) beginning behind the shoulders and extending along the dorsal midline. Hairs remarkably longer than remainder of back and flanks. Color of crest usually contrasts with ground color of dorsolateral pelage.

Throat: Two or three transverse dark stripes.

Chest and abdomen: Numerous dark spots, or transverse lines of dark spots.

Tail: Ringed or not, with either a dark or pale tip.

Legs: Two or three dark stripes usually present between elbow and wrist, and three to five between knee and ankle. These stripes usually form complete rings around the leg, but may be interrupted (incomplete) on inner surface.

Feet: In some forms, feet can be dark both on dorsal and ventral surfaces, or only below.

Description of basic spotting types. Analysis of spotting variability in my sample shows the three general patterns (types 1, 2, and 3) illustrated in figure 15. For two, I found some variation consisting of a graduated expression of the markings, described in types 2A to 2C, and 3A and 3B as follows:

Type 1— Characterized by oblique, rusty-cinnamon cheek stripes and lines on flanks, over a reddish or dark gray background (Wolffsohn, 1908, mentioned these two phases in central Chilean cats, only differing in the background color). The spinal crest is conspicuous, black and rusty, the pattern resulting from alternating black and orange color bands on each hair. Tail has four or five reddish rings, the last two appearing darker. Ears are cinnamon dorsally, with blackish edges and black tips. Ventral markings are rusty ochraceous, on a more or less white background. Rings and stripes on legs are dark brown, somewhat rustier-colored on hind legs. Feet are cinnamon dorsally, with small dark spots.

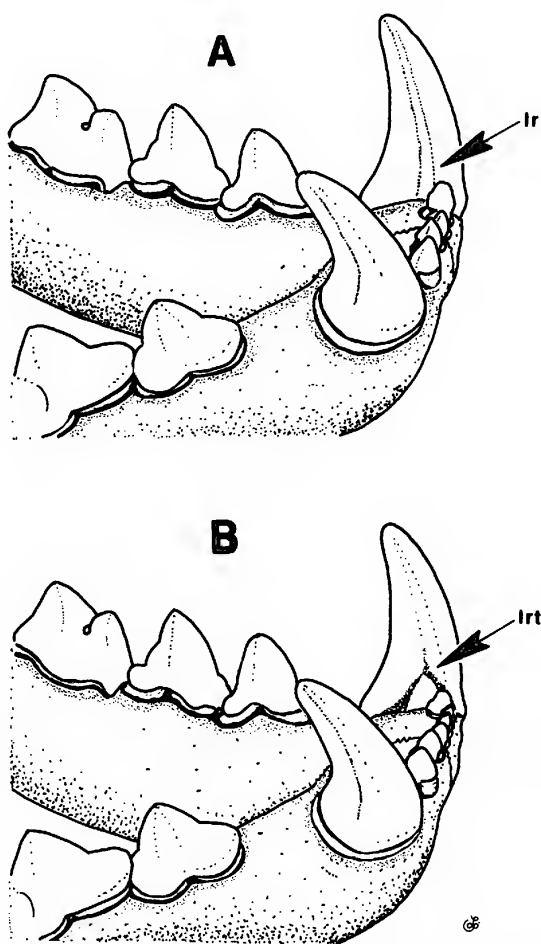


Fig. 14. All specimens show one lingual ridge (lr) on each lower canine (type 1), but only some of them show a tubercle on the basal portion of the ridge (lrt). (A) type 1; (B) type 2.

Todos los ejemplares muestran una cresta lingual (lr) en cada canino inferior (tipo 1), pero sólo algunos de ellos muestran un tubérculo en la parte basal de la cresta (lrt). (A) tipo 1; (B) tipo 2.

Type 2A— Characterized by large, reddish brown rosettes with darker borders, arranged in oblique chains along the flanks. Spinal crest and tail rings are same color as flank spots. Tail ringed from base to tip. Base of ears same color as head, otherwise ears are black with a small gray spot. Stripes on legs and the ventral markings are dark brown (almost black) on a more or less white background. Feet similar to the background color of the body, but with some small, dark spots on the dorsal surfaces.

TABLE 1

Values of 14 Cranial Measurements and One Ratio (in percent) for Adult Pampas Cats

Names of measurements and museum acronyms under Materials and Methods.

Valores de 14 Medidas Craneales y un Índice (en porcentaje) para Gatos de las Pampas Adultos. Nombres de las variables y abreviaturas de los museos en "Materials and Methods."

	Gender	GLS	CGL	RWC	MW	IOW	POW	ZW	P4L	ML	SCL/ GLS
Population 1											
USNM 391853	?	98.6	90.7	28.9	45.6	18.9	28.4	73.1	11.4	62.5	30
Population 2											
FMNH 24370	♂	107.5	99.4	26.1	46.0	21.6	29.2	—	12.4	68.8	39
BM 8.4.13.1	♂	108.0	99.7	26.0	47.5	20.9	29.3	77.6	12.3	70.4	30
BM 1.11.18.1	♂	110.1	100.4	26.5	47.0	22.0	30.7	79.3	11.4	70.4	46
BM 1.9.25.1	♂	104.1	95.4	25.2	48.5	19.8	28.7	78.8	12.2	65.9	50
BM 1.11.6.2	♂	107.0	97.7	27.0	48.9	22.7	28.6	84.3	11.8	69.5	53
BM 46.11.3.11	?	107.0	97.6	25.5	47.2	—	27.7	77.6	11.9	67.7	41
Population 3											
<i>Ecuador</i>											
— ^a	♂	88.0	82.0	—	—	16.5	24.8	64.0	10.0	—	—
FMNH 43291	♂	90.4	84.5	22.3	38.0	18.9	26.8	62.9	11.0	57.9	18
AMNH 76150	♂	90.7	84.7	23.1	38.7	18.8	27.8	65.5	11.1	57.3	15
<i>Peru</i>											
FMNH 52488	♂	98.0	90.5	24.2	42.0	18.3	29.6	72.0	11.3	63.4	22
MVZ 114942	♂	96.7	88.6	23.5	42.7	18.3	28.5	70.3	11.8	62.4	22
MVZ 114943	♂	100.8	92.1	23.1	42.6	21.0	27.2	71.8	11.2	64.6	25
FMNH 68318	♀	89.2	82.3	20.3	38.9	19.4	29.5	60.1	11.0	54.2	12
BM 27.11.1.67	♀	91.6	84.7	21.7	41.2	17.6	27.2	65.7	11.5	57.1	15
MVZ 114777	♀	97.1	88.8	22.7	45.0	18.2	30.2	69.9	11.6	62.6	18
MVZ 139613	?	96.2	89.0	22.7	41.2	17.1	27.6	64.3	11.2	61.5	18
<i>Bolivia</i>											
BM 34.9.2.31	♀	96.1	88.0	22.6	41.1	18.6	29.5	68.4	11.2	60.7	12
EBD 8741	?	101.4	94.2	25.3	43.1	20.7	26.0	73.3	12.0	64.8	17
<i>NW Argentina</i>											
BM 34.11.4.5	♂	103.2	94.4	25.0	43.7	19.0	27.8	72.5	12.6	65.5	17
MACN 30103	♀	96.3	88.8	25.1	42.5	19.1	29.0	70.6	12.0	63.5	18
MACN 17816	?	101.9	94.1	25.6	45.6	19.7	27.8	76.0	11.7	65.0	24
<i>C + S Argentina</i>											
AMNH 16695	♂	109.0	99.3	26.5	49.6	22.3	29.0	78.9	11.8	71.5	16
BM 55.12.24.261	♂	104.7	—	24.3	47.4	19.8	28.9	71.5	13.0	67.2	18
MACN 16489	♂	109.2	99.0	26.3	50.9	—	—	79.2	11.0	69.0	21
BM 12.7.12.4	♀	97.3	90.3	22.8	45.7	—	29.6	70.9	11.3	63.8	12
BM 21.6.7.5	♀	94.4	87.9	23.6	43.8	21.1	29.4	72.5	11.6	61.4	10
USNM 172786	?	92.7	84.0	22.1	42.3	—	28.2	67.8	11.1	59.8	14
BM 3.2.24.1	?	102.7	93.7	23.7	45.0	19.9	28.7	69.2	12.0	65.3	12
Population 4											
AMNH 133977	♂	96.6	91.8	21.9	39.3	17.8	27.4	63.3	11.6	60.9	9
AMNH 354	♂	94.3	89.4	21.6	39.2	18.3	29.7	62.1	11.6	59.4	16
AMNH 243110	♂	98.7	91.1	23.0	41.6	17.6	29.1	67.5	11.4	63.8	11
Population 5											
AMNH 189394	♂	100.5	91.8	24.1	42.9	17.2	—	65.4	13.0	62.5	9
MNCNM 884 ^b	♀	—	—	—	—	—	—	66.7	11.0	58.8	—

^a Lönnberg, 1913.^b Ximenez, 1961.

TABLE 2
Values for Five External Measurements of Adult Pampas Cats

Names of measurements and museum acronyms under Material and Methods.

Valores de Cinco Medidas Externas para Gatos de las Pampas Adultos. Nombres de las variables y abreviaturas de los museos en "Materials and Methods."

	Gender	HB	T	HF	E	W
Population 2						
— ^a	♂	670	290	120	57	—
BM 8.4.13.1	♂	567	322	139	61	—
BM 1.12.27.1	♂	559	280	130	62	—
BM 1.9.25.1	♂	595	325	128	60	—
BM 1.11.6.2	♂	642	295	118	65	—
Population 3						
<i>Ecuador</i>						
— ^b	♂	510	270	—	—	—
<i>Peru</i>						
FMNH 68381	♀	464	240	105	50	—
BM 27.11.1.67	♀	520	280	118	49	—
<i>Bolivia</i>						
BM 34.9.2.31	♀	750	285	115	55	—
<i>NW Argentina</i>						
BM 34.11.4.5	♂	633	281	133	46	—
MACN 30103	♀	535	266	122	46	—
<i>C + S Argentina</i>						
BM 55.12.24.261	♂	650	279	—	48	—
MLP 8639 ^c	♀	540	230	120	45	—
Population 4						
<i>Brazil</i>						
AMNH 133977	♂	560	330	130	34	—
AMNH 354	♂	467	230	—	—	—
<i>Paraguay</i>						
AMNH 243110	♂	523	279	127	53	2900
Population 5						
<i>Uruguay</i>						
MNCNM 884 ^d	♀	532	292	121	52	—

^a Wolffshon, 1923.

^b Lönnberg, 1913.

^c Cabrera, 1961.

^d Ximenez, 1961.

Type 2B— It is possible to recognize the pattern described for type 2A, but body markings and tail rings are paler and less conspicuous, and background color is also paler. Stripes on front legs are dark brown, like those in type 2A, but paler on hind legs.

Type 2C— Specimens are almost uniformly grayish, usually with no signs of dorsal spots or rings on body and tail, although some

individuals show indistinct oblique darker lines on flanks. Stripes on front and hind legs are conspicuous and dark brown, as are ventral markings.

Type 3A— Specimens of this type exhibit an almost uniform brown agouti color dorsally, with some traces of dark brown rosettes on the flanks. Spinal crest is a little darker than ground color. Tail not ringed, black at

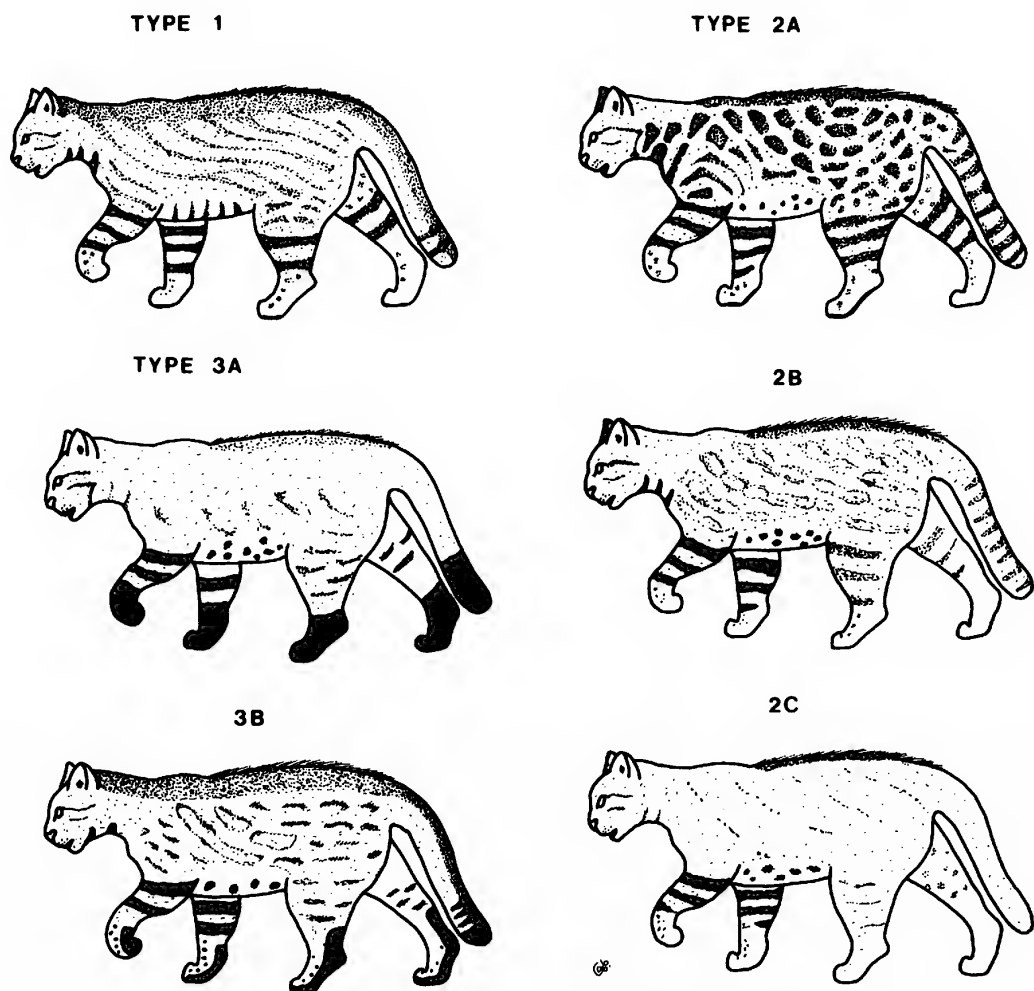


Fig. 15. Three basic types of coat pattern identified, and their variation.
Los tres tipos básicos de diseño del pelaje identificados y su gradación.

the tip. Ears tricolor with a black band along anterointernal border, reddish on basal portion, and creamy-white over the remaining outer surface. Leg stripes and ventral markings are black. Throat is white, becoming orangish behind the first throat stripe, and over all other ventral surfaces. Feet are dorsally and ventrally black, including wrists and ankles (fig. 15).

Type 3B— Similar to type 3A, although background color generally paler, more yellowish on back and flanks. Spots on the flanks are more conspicuous (brown) than in type 3A. Leg stripes and ventral markings are similar to those of type 3A. Feet are black only on palmar and plantar surfaces. Black tip of

tail less extensive than in type 3A and, in part, consisting of discontinuous rings.

Geographic variation. The different coat pattern types are distributed geographically. I did not find any significant geographic variation among specimens showing the type 1 pattern. For type 2, I found a gradation (fig. 15, 2A–2C) in the level of expression of markings related to latitude and elevation (table 3, fig. 16). Specimens from the northern parts of the distribution (near the equator) have the type 2A pattern, while specimens inhabiting the southern parts (up to 47° S) show the type 2C pattern. I found type 2B only in the area between 22 and 39° S, where specimens of pattern types 2A and 2C also

TABLE 3

Variation of Type 2 Coat Pattern in Relation to Latitude, Elevation, and Habitat
Variación del Tipo 2 de Diseño del Pelaje, en Relación con la Latitud, Altitud y Tipo de Hábitat.

Lat (°S)	Alt. (m)	Pattern	Habitat
0	5704	2A	Highland shrub steppes
0	3660	2A	Highland shrub steppes
0	2818	2A	Highland shrub steppes
5	2134	2A	Forests in dry inner Andean valleys
10	2064	2A	Highland shrub steppes and grasslands
10	2745	2A	Highland shrub steppes and grasslands
13	3500–4000	2A	Highland shrub steppes and grasslands
14	4390	2A	Highland shrub steppes and grasslands
17	4000	2A	Highland shrub steppes and grasslands
22	3000–5000	2A	Highland shrub steppes and grasslands
22	565	2B	Dry forests and savannas
24	5000	2A	Highland shrub steppes and grasslands
23–25	2500	2B	Highland shrub steppes and grasslands
27	1800	2B	Highland shrub steppes and grasslands
27	400	2B	Dry forests and savannas
28	501	2B, 2C	Dry forests and savannas
29	1240	2A	Dry shrub steppes
29	1000–4000	2A	Highland shrub steppes and grasslands
30	279	2B	Dry forests and savannas
36	311	2B	Dry forests and savannas
36	302	2C	Dry forests and savannas
36	190	2B	Dry forests and savannas
38	150	2B	Dry forests and savannas
38	100–200	2B	Dry forests and savannas
39	1000	2B	Patagonian shrub and grass steppes
40	767	2C	Patagonian shrub and grass steppes
40	502	2C	Dry shrub steppes
40	sea level	2C	Dry forests and savannas
41	950	2C	Patagonian shrub and grass steppes
41	888	2C	Dry forests and savannas
45	200–500	2C	Patagonian shrub and grass steppes
47	sea level	2C	Patagonian shrub and grass steppes

occur. This latitudinal range covers the transitional zone where distributions shift from highland steppe to lower elevation dry forest and shrubland.

The variants of type 3 (fig. 15: types 3A and 3B) represent two expressions of the same pattern. I did not find intermediates.

HABITATS

I examined phytogeographic and climatic characteristics of the localities (information mainly from Hueck and Seibert, 1972) to identify potential patterns of habitat preference, as well as constraints affecting the distribution of these cats.

My general descriptions of the phytogeo-

graphic units (after Hueck and Seibert, 1972; Cabrera, 1976; Pearson, 1980; Mares et al., 1989; and Johnson et al., 1990) are given below. They include vegetation type, elevational range (in meters), annual average temperature (degrees Celsius), and annual rainfall (in millimeters).

Páramos: Shrub steppes (3200) 3800–4700 m, 1–10°C, 1000–2300 mm.

Forests in dry inner-Andean valleys: 400–2000 m, 16–27°C, 300–800 mm.

Andean highlands: Shrub steppes and grasslands, elevation between 3000 and 4000 m in the north, and 600 and 1500 m in the south, variable temperatures and rainfall depending on latitude and elevation.

Puna: Open shrub steppes and grasslands

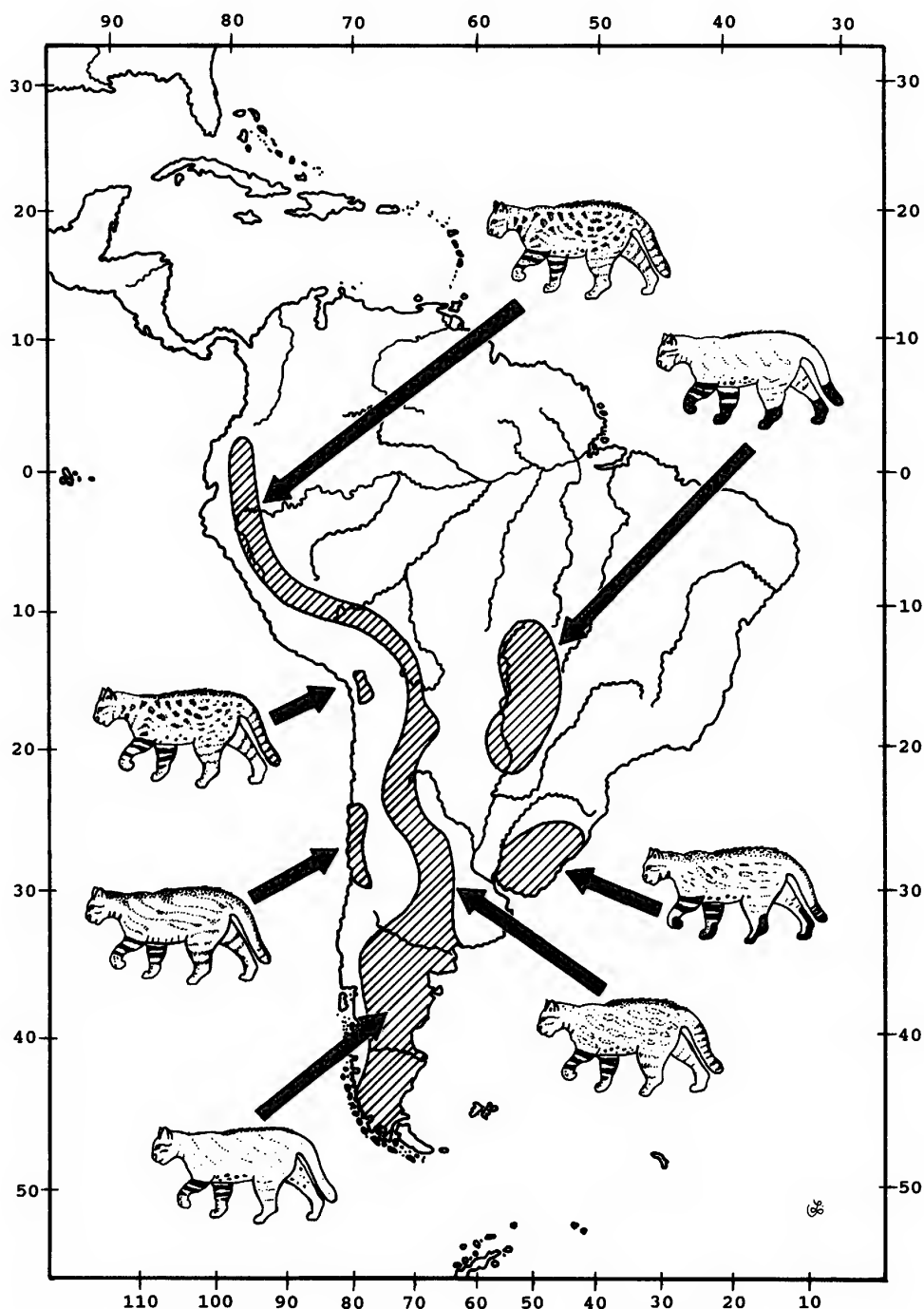


Fig. 16. Geographic distribution of the different types of coat pattern identified.
Distribución geográfica de los diferentes tipos de diseño del pelaje identificados.

between 3400 and 4300 m, and grass steppes above 4300 m (limit 4500 m), 3–10°C, 100–500 mm.

Chaco: Dry forests and savannas, from < 100 to 500 m, 19–24°C, 500–1000 mm.

Espinal: Dry forests, sea level to 400 m, 14–18°C, 300–600 mm.

Monte: Dry shrub steppes, sea level to 1000 m, 14–20°C, 100–350 mm.

Cerrado: Dry tree/shrub savannas, open

canopy, 200–600 m, 24–27°C, 1100–2000 mm.

Campos limpos and sujos: Open grasslands with small shrubs, 500–2000 m, 24–27°C, 1100–2000 mm.

Pantanal: Mesic savannas, almost totally inundated during the rainy season, 100–200 m, 24–27°C, 1200–1400 mm.

Upland mesophytic forests: With well-developed canopy, 200–500 m, 24–25°C, 1100–2000 mm.

Subtropical xerophytic, sclerophyll forests: Sea level to 1900 m, 13–15°C, 150–1500 mm.

Pampas: Grass and shrub steppes, grasslands, sea level to 1200 m, 14–19°C, 700–1300 mm.

Patagonian steppes: Shrub and grass steppes, humid grasslands, sea level to 1500 m, 5–14°C, 100–600 mm.

According to my samples, the following groups show habitat affinity:

1) Cats living in highlands from Ecuador to NW Argentina (northern part of population 3), as well as northern Chile (population 1), inhabit areas of shrub and grass steppes (páramos and marginal areas of the puna), and occasionally penetrate dry forests in the upper part of inner Andean valleys. Elevation ranges from 1800 to 5000 m, based on elevations recorded by collectors; elevations found in bibliographic sources often refer to elevational ranges in mountains, or to a gradient between topographic lines. These areas are cold (1–10°C), but can be milder in valleys (16–27°C). Annual rainfall is variable (100–2300 mm). Specimens from northern Chile have been collected on the western slope of the Andes. All other populations live either on the eastern slope of the Andes or farther east.

2) Animals living in lowlands of northwestern and central Argentina (central part of population 3), as well as in Uruguay and southern Brazil (population 5) inhabit grasslands (pampas), dry and mesophytic forests (chaco and espinal), shrubland steppes (monte), and transitional areas. Specimens from these areas came from elevations ranging from sea level to 1240 m. Temperatures are moderate (14–24°C) and annual rainfall varies from 300 to 1300 mm (100–350 mm in monte).

3) Cats from southern Argentina and Chile

(southern range of population 3) inhabit the shrubland and grassland steppes of Patagonia. Specimens from this area ranged from sea level to 1100 m. The temperature is low, 0–13°C, and annual rainfall is 100–600 mm.

4) Animals living in central Chile (population 2) inhabit subtropical, xerophytic forests, occasionally penetrating the spiny shrublands to the north. Collecting localities range from sea level to 1800 m. Temperatures vary from 13 to 15°C, and annual rainfall from 150 to 1500 mm. This population lives on the western slope of the Andes.

5) Cats from southwestern Brazil and Paraguay (population 4) inhabit shrubland and grassland steppes (campos limpos and sujos), dry savannas (campos cerrados), humid savannas (pantanal), and deciduous forests. Specimens have been collected between 142 and 793 m above sea level. Temperatures range from 20 to 27°C, and annual rainfall varies from 1100 to 2000 mm.

TAXONOMIC ACCOUNTS

The genus *Lynchailurus*

Lynchailurus Severtzov, 1858: 385. Type species *Felis pajeros* Desmarest, 1816, by monotypy.
Pajeros Gray, 1867: 269. Type species *Pajeros pampanus* Gray, 1867, by monotypy.

The Pampas cats have been included either in the monotypic genera *Lynchailurus* (most authors prior to Corbet and Hill, 1980), or *Panthera* (Fitzinger, 1869), or *Pajeros* (Gray, 1867); in the genus *Felis* Linnaeus, 1758 (mostly after Corbet and Hill, 1980); in the genus *Leopardus* Gray, 1842 (e.g., Herrington, 1985; Salles, 1992); or in the genus *Oncifelis* Severtzov, 1858 (e.g., Wozencraft, 1993). Some authors included *colocolo* under *Oncifelis* (e.g., Allen, 1919), or *Montifelis* Schwangart, 1941, or *Colocolo* Pocock, 1941, but the species they had in mind was actually *O. jacobitus* (Cornalia, 1865). Antonius (1933) proposed for *Felis braccatus* (Brazilian pampas cat) the subgenus *Mungofelis*. Other authors (Pocock, 1917) included *Dendrailurus* Severtzov, 1858, as a synonym of *Lynchailurus*, an error because the type species of *Dendrailurus* (*F. strigilata* Wagner, 1841) is based on Hamilton-Smith's (*in* Griffith, 1827) unidentifiable drawing of an animal from Guyana.

These different associations of names reflect uncertainty about the relationships between Pampas cats and other South American cats. I found three closely related species (see next section) that show affinities in morphology and habitat preference not shared with other cats, supporting the conclusion that the Pampas cats should be recognized as a separate genus, for which the oldest available name is *Lynchailurus* Severtzov, 1858.

Lynchailurus differs from other South American genera by the spinal crest of conspicuously long dark hairs that extends from behind the shoulders to the base of the tail; the large anterior chamber of the bulla due to the posteroventral hypertrophy of the ectotympanic; and ridges present on both sides of the upper canines. Other distinctive characters include inconspicuous tail rings; a variable pattern of dorsal spotting, ranging from large rosettes to faint, almost invisible oblique lines; the presence of several dark rings on front and hind legs, and several transverse dark stripes on the throat. Many of these characteristics were described by Pocock (1917, 1941).

Lynchailurus representatives are found from sea level to 5000 m. Collection localities at high elevations are usually on the marginal areas of the puna, and it is possible that these cats do not penetrate into that habitat because of competition with the Andean mountain cat, *O. jacobitus*.

SPECIES

With felids, it is often difficult to find morphological characters that are completely diagnostic, especially in closely related species, because atypical character states commonly appear at low frequency. For this reason, distinctive morphological gaps in single character states may not prove useful for detecting genetic discontinuities between species. I have found, however, that sets of character states can be used to assign specimens to species. This problem has been described for lynxes (Garcia-Perea et al., 1985; Garcia-Perea, 1991), especially in the two Palearctic species, *Lynx pardinus* and *L. lynx*, where only one of the morphological characters examined allowed full separation of the two.

Out of 13 morphological characters (table

4), I found five characteristic of the "colocolo" group (populations 1 and 2), two characterizing the "pajeros" group (population 3), and five distinguishing the "braccatus" group (populations 4 and 5). The three groups also differ in habitat preference. Although one can argue that the apparent allopatric distribution of these groups makes it difficult to decide whether they represent species or well-established subspecies, the level of differentiation relative to that seen in other felid groups recommends specific separation. The level of geographic variation observed within the "pajeros" group and the moderate variation shown within the less extensive "braccatus" and "colocolo" populations suggest that they have been genetically isolated for a long period. The extent of variation within each is comparable to that found between recognized subspecies in other felids. Further studies (e.g., molecular and cytogenetic) are desirable to test these taxonomic hypotheses. The taxonomic arrangement and species-level nomenclature is as follows. Synonyms are given under subspecies in the taxonomic summary.

Lynchailurus colocolo (Molina, 1782)

Felis colocola Molina, 1782: 295.

HOLOTYPE: Not designated.

TYPE LOCALITY: "Boschi del Chili," restricted to "province of Valparaiso" by W. H. Osgood (1943).

COMMON NAME SUGGESTED: Colocolo.

DIAGNOSTIC CHARACTERS: See table 4.

DISTRIBUTION: Highlands of northern Chile and forests of central Chile (western slope of the Andes).

REMARKS: The local names for this cat are "huiña" and "gato montés." Because the former also is applied to *F. guigna*, and the latter to *F. geoffroyi*, I suggest "colocolo" to avoid confusion.

Lynchailurus pajeros (Desmarest, 1816)

Felis pajeros Desmarest, 1816: 114.

HOLOTYPE: Not designated.

TYPE LOCALITY: Based on Azara's account (1802: 160) "Pajero" is "las pampas de Bue-

TABLE 4
Summary of the Characteristics of the Three Species of *Lynchailurus*
Resumen de las Características de las Tres Especies de *Lynchailurus*

	<i>Colocolo</i> ^a	<i>Pajeros</i> ^b	<i>Braccatus</i> ^c
Ectotympanic	Type 1	Type 2	Type 3
Mastoid process	Type 2	Type 1	Type 1
Palate, notch for postpalatine vein	Type 1	Type 1	Type 2
Palate, posterior edge	Type 2 (70%)	Type 1	Type 1
Type D sagittal crest	Yes	No	No
Inferior oblique muscle fossa	Type 2	Type 1	Type 1
Frequency, P2	Low	0	High
Shape, P3 paracone	Type 1	Type 1	Type 2
Parastyle on P3	No	No	Yes
Frequency, P4 protocone	75%	83%	80%
Lingual cusp, lower canine	No	Yes, very low frequency	Yes, high frequency
Coat pattern	Types 1, 2A	Type 2	Type 3
Body size	Large	Small to large	Medium
Distribution	N and C Chile	Ecuador, Peru, Bolivia, Argentina, S Chile	Brazil, Paraguay, Uruguay
Side of Andes	West	East	East
Habitat	N: Highland steppes C: Subtropical forest	Grass and shrub steppes, dry forests	Grass and shrub steppes, humid savannas, deciduous forests
Elevation (m) range	N: 2000–4000 C: 0–1800	0–5000	0–793

^a Populations 1 and 2.

^b Population 3.

^c Populations 4 and 5.

nos Ayres, entre los 35 y 36 grados,” Argentina.

COMMON NAME: Pampas cat, gato de las pampas.

DIAGNOSTIC CHARACTERS: See table 4.

DISTRIBUTION: Highlands on the eastern slope of the Andes in Ecuador, Peru, Bolivia, and northwestern Argentina; lowlands of northwestern, central, and southern Argentina; and Chilean Patagonia.

REMARKS: The type locality corresponds to the specimens described by Azara (1802: 160), on which Desmarest based his *Felis pajeros*. Most authors cited Azara's (1801: 114) description of “Le Chat Pampa” as the basis of Desmarest's (1816: 114) description of *Felis pajeros*, and mentioned Paraguay as the type locality (e.g., Olfers, 1818; Lesson, 1827). Nevertheless, Desmarest cited “le Pajeros de d’Azara” (from Azara, 1802) as the basis of his short description.

Lynchailurus braccatus (Cope, 1889)

Felis braccata Cope, 1889: 144.

HOLOTYPE: AMNH 354. Adult male collected by E. D. Cope in November, 1884.

TYPE LOCALITY: “The province of Rio Grande do Sul, or in Matto Grosso,” restricted by J. A. Allen (1919: 378) to “Chapada, Mato Grosso,” Brazil.

COMMON NAME SUGGESTED: Pantanal cat.

DIAGNOSTIC CHARACTERS: See table 4.

DISTRIBUTION: Paraguay, Uruguay, and southwestern and southern Brazil.

COMMENTS: The local name for this cat is “gato palheiro,” but because it can be confused with *L. pajeros*, I propose the common name “Pantanal cat” (although this species does not live exclusively in pantanal areas, it is the only species of this group occurring there).

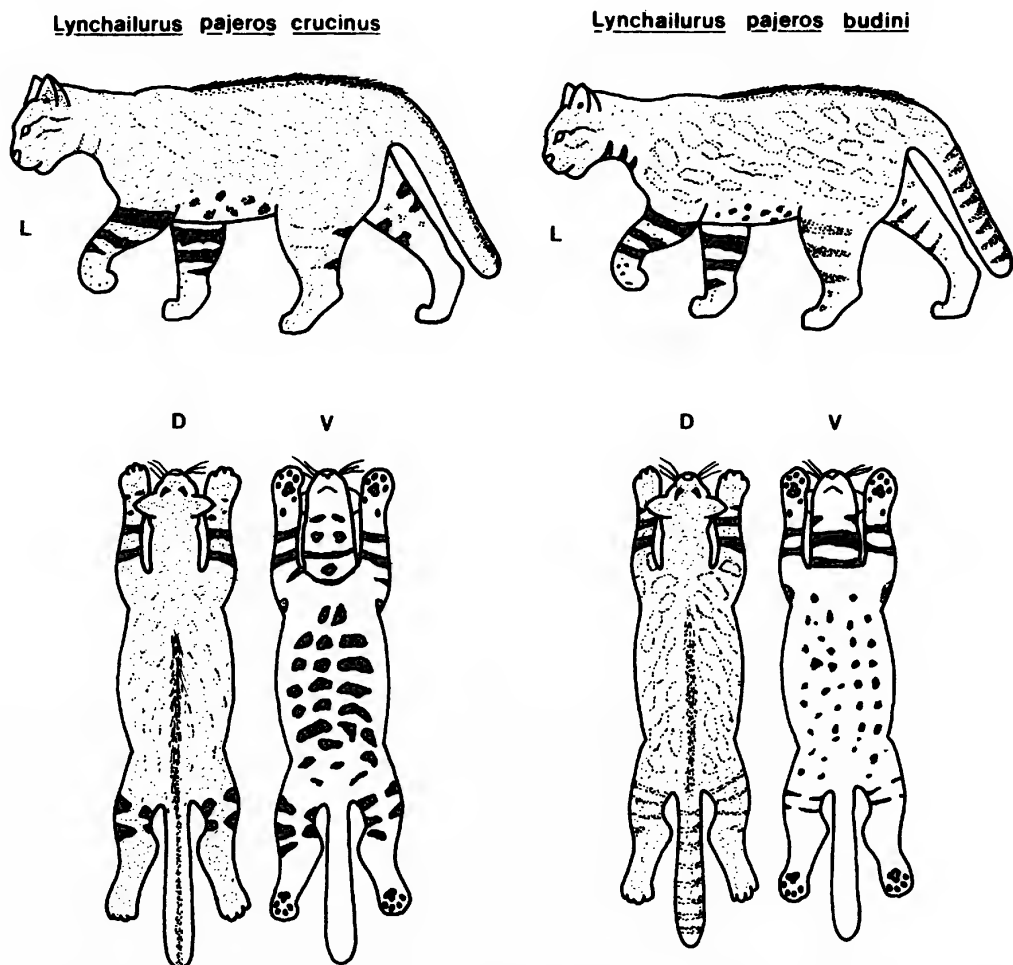


Fig. 17. Types of coat pattern characterizing three subspecies of *Lynchailurus pajeros*.
Tipos de diseños del pelaje que caracterizan a tres subespecies de *Lynchailurus pajeros*.

SUBSPECIES

Observations, along with the original descriptions of the subspecies, provide information about the taxonomic identity of some populations. However, my sample was not large enough to re-evaluate all of the subspecies described. This will require larger samples from throughout the distributional range of the group.

The most problematic question is how many subspecies are referable to the species *L. pajeros*, since available data suggest clinal variation from north to south in morphological characters. There seem to be three groups showing habitat affinities and morphological similarities (northern, central, and southern),

but the small sizes of the samples analyzed for the different subspecies prevent making more objective determinations.

Populations from Ecuador and Peru, assigned to *thomasi* Lönnberg, 1913, and *garleppi* Matschie, 1912, respectively, have similar patterns of pelage markings (type 2A; fig. 17) and cranial morphology; they also live in similar habitats (steppe highlands). However, specimens of *thomasi* are conspicuously smaller than those of *garleppi*, and their ectotympanic chamber is smaller (close to that of *braccatus*). Therefore, I recognize these two morphotypes as representing different subspecies.

Specimens from Bolivia are assigned to *steinbachi* Pocock, 1941. The two skulls in

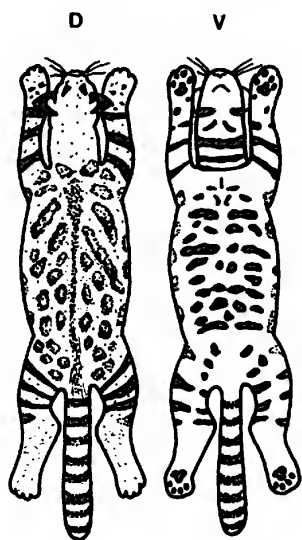
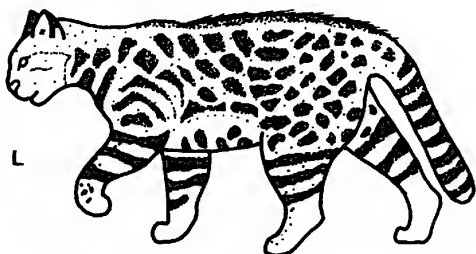
Lynchailurus pajeros thomasi

Fig. 17. Continued.

my sample are larger than skulls of *garleppi* from neighboring Peru. Coloration of the rosettes is also paler. There is not enough information to fully evaluate the validity of this subspecies, and until more specimens are studied, I treat it as a separate taxon.

Populations living in mountainous areas of northwestern Argentina and assigned to *budini* Pocock, 1941, and *crespoi* Cabrera, 1957, show several degrees of fading of pelage markings (types 2A to 2C; fig. 17). These forms live in a transitional area where the habitat shifts from steppe highlands to dry forested lowlands. When Cabrera (1957) described *crespoi*, he said his specimen came from Aguaray's chaco, but later, in his catalog of South American mammals he noted that the habitat of this form is in the humid forests

of Tucumán and Salta, with no mention of new specimens. His information is not consistent with the data obtained from my sample and because Cabrera never explained this change, I am relying on his primary information (chaco region). Similarity in external characters and habitat suggests that *crespoi* may be a synonym of *budini*, but I would need more specimens from the type locality of *crespoi* (only known from the type specimen, a skin in bad condition), to determine if it agrees with *budini* or not.

The population from central Argentina is the nominal subspecies of *L. pajeros* (Desmarest, 1816). Color in this population is distinctive. The coat pattern shows the types 2B and 2C, but the color has an overall orangish hue and the ventral markings are orange. According to my sample, its distribution is limited to La Pampa province (espinal forest). However, the type locality (pampas of Buenos Aires between 35 and 36°S) is farther east (fig. 18). Azara's (1802) description of the "pajero" agrees with the characteristics of my specimens, and it is unlikely that he erred in the locality because he collected the specimens himself. Obviously, the distributional range of this population has been reduced substantially during the last two centuries.

Animals from southern Argentina are assigned to *crucinus* Thomas, 1901. Pelage is always type 2C (fig. 17) with the typical grayish color. The body size is the largest of *L. pajeros*, and the ectotympanic chamber is larger than in typical *pajeros*. The subspecific separation of *crucinus* and *pajeros* is justified. The population in southern Chile should be included in the subspecies *crucinus*.

Brazilian specimens are assigned to *braccatus* Cope, 1889. Matschie (1912) described *Felis (Lynchailurus) colocola neumayeri* (holotype ZMB 34506), based on one specimen supposedly collected in Rio das Mortes, Mato Grosso (Brazil, close to the type locality of *braccatus*). Allen (1919) and Pocock (1941) considered *neumayeri* as a form of *O. jacobitus* (called by them *colocolo*), and Cabrera (1958) treated it as a synonym of *braccatus*. Matschie's description indicates that his specimen is not related to *braccatus*. Its external measurements (head + body 850 mm, tail 410 mm) and some characteristics of the coat pattern (two dark stripes on the front,

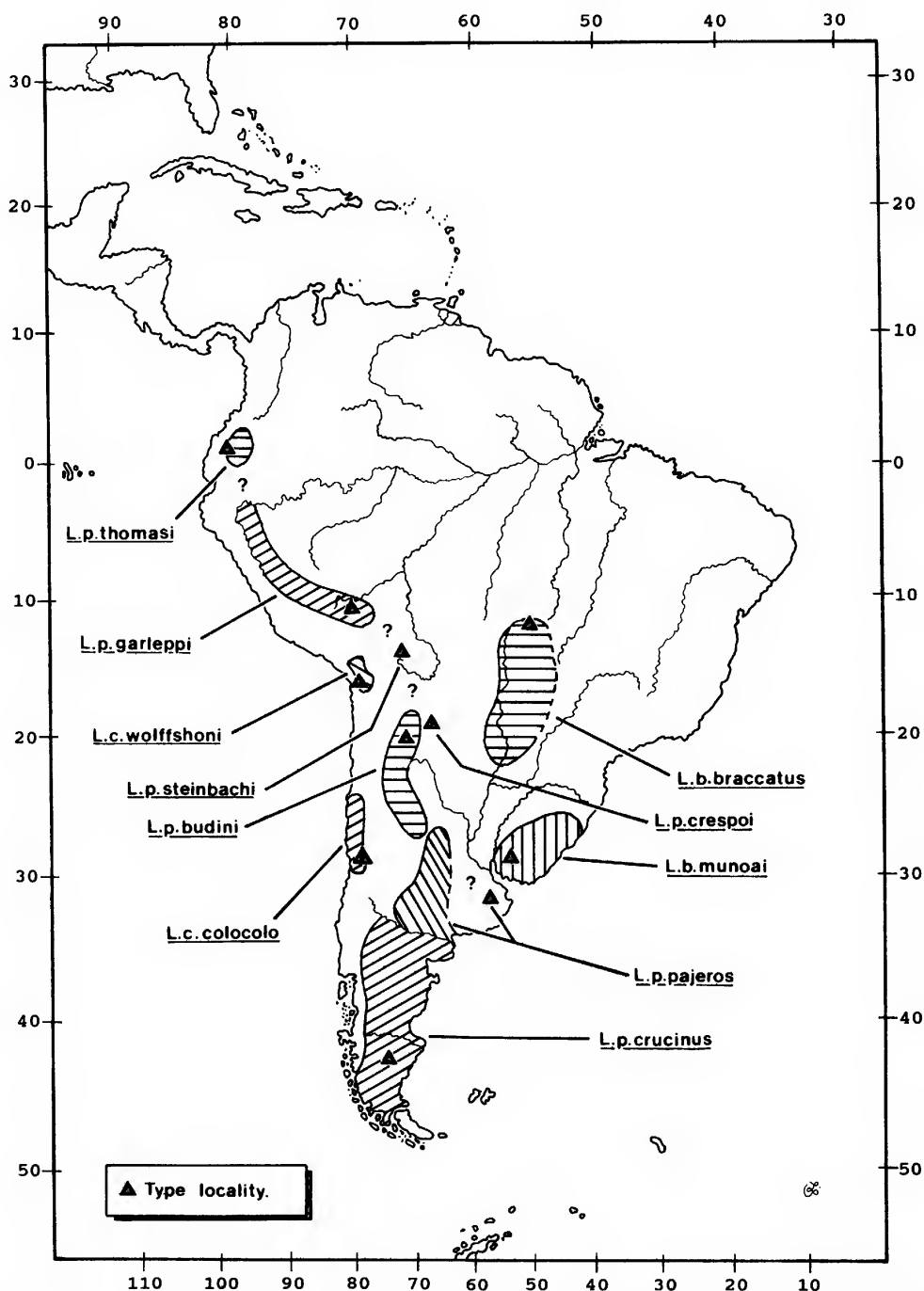


Fig. 18. Striped areas represent approximate ranges of the different subspecies of these groups. Black triangles: type localities.

Las áreas rayadas representan las áreas aproximadas de distribución de las diferentes subespecies de este grupo. Triángulos negros: localidades típicas.

with several small spots between them; eight ochraceous tail rings; pale gray feet; large spots between the shoulders forming bands) do not

fit into *braccatus*, but they could well fit *jacobitus*. Schwangart (1941) and Mann (1945) identified the specimen as *jacobitus*, suggest-

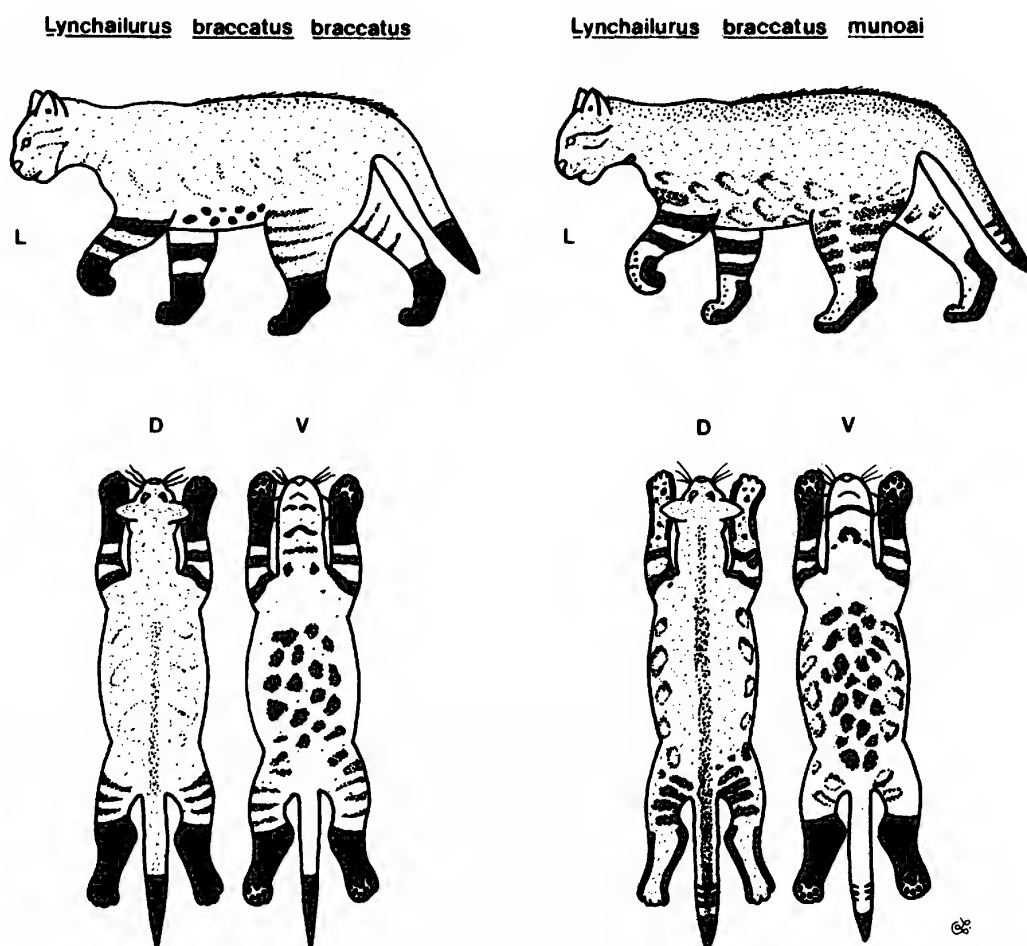


Fig. 19. Types of coat pattern characterizing the two subspecies of *Lynchailurus braccatus*. (L) lateral view; (D) dorsal; (V) ventral.

Tipos de diseños del pelaje que caracterizan a las dos subespecies de *Lynchailurus braccatus*. (L) aspecto lateral; (D) dorsal; (V) ventral.

ing that the locality in the label is wrong, because *jacobitus* inhabits only high-altitude steppes of the Andes in Peru, Bolivia, Chile, and Argentina. *L. braccatus braccatus* shows coat pattern type 3A (fig. 19), and occurs in warmer and more humid habitats than do other congeners. My observations indicate that animals from Paraguay should be assigned to *braccatus*. Two of the Paraguayan records included in Redford and Eisenberg (1992) could be misidentified specimens (see Appendix 2).

Specimens from Uruguay are assigned to *munoai* Ximenez, 1961. The morphological differences between the skulls of *braccatus* and *munoai* are not distinctive, although some

variation exists in coat pattern (type 3B in *munoai*, fig. 19) and in body size (*munoai* is larger). In addition, the ranges of *braccatus* and *munoai* are separated by rainforest. Therefore, it is reasonable to retain *munoai* as a separate subspecies. The specimen collected by Ihering (1911) in São Lourenço (Rio Grande do Sul) is assignable to *munoai*.

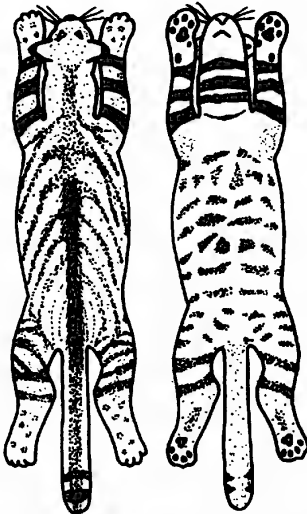
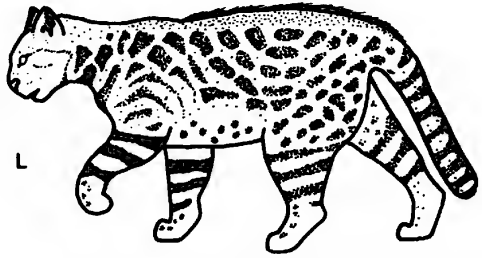
Pocock (1941) described *huina* for the population living in central Chile, but it is a synonym of Molina's *colocolo*. This population is characterized by coat pattern type 1 (fig. 20). Its size is largest for the genus and it occupies subtropical xerophytic forests.

The population in northern Chile has been assigned to *garleppi* by Osgood (1943), to

Lynchailurus colocolo colocolo

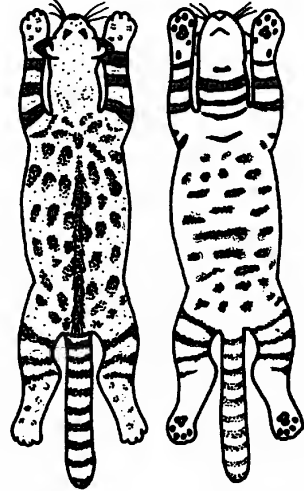
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Lynchailurus colocolo wolffsohni

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Fig. 20. Types of coat pattern characterizing the two subspecies of *Lynchailurus colocolo*. (L) lateral view; (D) dorsal; (V) ventral.

Tipos de diseños del pelaje que caracterizan a las dos subespecies de *Lynchailurus colocolo*. (L) aspecto lateral; (D) dorsal; (V) ventral.

budini by Cabrera (1961), and to *colocolo* by Mann (1945). Osgood (1943) noted a problem in identifying a specimen of this population at subspecies level and said that it "perhaps will prove nearer to *garleppi* than *colocolo*." Coat pattern of this population (type 2A; fig. 20) is similar to that of *garleppi*. However, examination of cranial characteristics indicates that specimens from northern Chile are closer to the central Chilean specimens than to *garleppi* or any other known population of *Lynchailurus* (table 3). In addition, this population lives on the west drainage of the Andes, as does the central Chilean population, in isolation from *garlep-*

pi and *budini* from the eastern slope. For these reasons, I assign this population to *L. colocolo*, but as a subspecifically distinct population. Differences include minor variation in the ectotympanic and paroccipital processes, different coat patterns (type 2A in the northern form), and different habitat preferences. This population is separated by nearly 2000 km from the central Chilean population. Because the population from northern Chile does not yet bear a name, I propose the following name:

Lynchailurus colocolo wolffsohni,
new subspecies

HOLOTYPE: USNM 391853 (National Museum of Natural History, Washington DC, USA), adult specimen of unknown sex (skin and skull) collected on the río Camarones, provincia Tarapacá, between 2000 and 4000 m, Chile, donated by G. Mann in 1949.

OTHER SPECIMEN: FMNH 24358 (Field Museum of Natural History, Chicago), juvenile male still replacing the milk dentition (skull and skin) collected in Putre, Tacna (Chile), at 13,500 ft, by C. C. Sanborn, on the 28th of June, 1924.

DIAGNOSIS: A subspecies of *Lynchailurus colocolo*, with coat pattern similar to that found in *L. pajeros garleppi*, characterized by large, reddish brown rosettes, darker in their borders, running in oblique chains along the flanks; spinal crest and tail rings same color as flank spots; tail ringed from the base to the tip (usually 8 rings); ears dorsally black with a small gray spot; stripes on the legs (2 or 3 on front legs, 3 to 5 on hind legs) and ventral markings dark brown, almost black, on a white background. Cranial characteristics are typical for the species *L. colocolo*, with a large ectotympanic chamber (representing 40% of bullar volume); mastoid process well developed posteriorly; posterior edge of the palate U-shaped, with no medial notch in adults; sagittal crests well developed, occupying most or all of the parietal suture; presence of upper premolar. Differs from nominal subspecies in type of coat pattern, in having smaller ectotympanic, and in having less extensive mastoid processes.

MEASUREMENTS: The only adult specimen examined (holotype) is of unknown sex and has no external measurements. It has the following cranial measurements: GLS 98.6, CBL 90.7, RWC 28.9, MW 45.6, IOW 18.9, POW 28.4, ZW 73.1, P4L 11.4, ML 62.5, SCL/TL 30.

HABITAT: Highland shrub and grass steppes (páramos, marginal areas of puna) on the west side of the Andes, between 2000 and 4000 m altitude.

ETYMOLOGY: The name "wolffsohni" is a tribute to John A. Wolffsohn, who significantly contributed to the knowledge of Chilean colocolos.

COMMENTS: The label of the type specimen indicates "Camarones, Tarapacá, Chile." The type locality may be regarded as "río Ca-

marones, provincia Tarapacá, between 2000 and 4000 m, Chile" based on the information provided by Mann (1945: 28). He collected specimens (probably including the holotype) of this subspecies at the type locality, and indicated that this cat lives in "los contrafuertes andinos, cuyo territorio se establece ya a unos 2000 metros para elevarse hasta 4000 metros de altura."

TAXONOMIC SUMMARY

Geographic locations of the different subspecies mentioned below are illustrated in figure 18.

Lynchailurus colocolo (Molina, 1782)

One doubtful subspecific name included in this species is *Panthera maracaya albescens* Fitzinger, 1869: 232.

L. c. colocolo (Molina, 1782)

Felis colocola Molina, 1782: 295.

Felis colorolla Bechstein, 1800: 699 (in Cabrera, 1958).

Felis colocolo Molina, 1810: 245.

Lynchailurus pajeros huina Pocock, 1941: 261 (type locality, "The range of mountains over Lake Catapilco, near Aconcagua, 900 m"; holotype BM 1.11.6.2).

HOLOTYPE: Not designated.

TYPE LOCALITY: "Province of Valparaíso," Chile.

RANGE: Central Chilean provinces, from Coquimbo probably to Concepción (Wolffsohn, 1908).

L. c. wolffsohni, new subspecies

HOLOTYPE: USNM 391853.

TYPE LOCALITY: Río Camarones, provincia Tarapacá, between 2000 and 4000 m, Chile.

RANGE: Highlands of Tarapacá province (N Chile), western slope of Andes.

Lynchailurus pajeros (Desmarest, 1816)

L. p. budini Pocock, 1941

Lynchailurus pajeros budini Pocock, 1941: 263.

HOLOTYPE: BM 34.11.4.5.

TYPE LOCALITY: "Mount Sola, 2500 m, in Salta, northern Argentine."

RANGE: Mountains of northwestern Argentina, eastern side of Andes.

L. p. crespoi (Cabrera, 1957)

Felis (*Lynchailurus*) *colocolo crespoi* Cabrera, 1957: 71.

HOLOTYPE: MACN 36230.

TYPE LOCALITY: "Aguaray, provincia de Salta," Argentina.

RANGE: Only known from the type locality.

L. p. crucinus (Thomas, 1901)

Felis pajeros crucina Thomas, 1901: 247.

HOLOTYPE: BM 55.12.24.261.

TYPE LOCALITY: "Santa Cruz," Argentina.

RANGE: Southern half of Argentina, and Chilean Patagonia.

L. p. garleppi Matschie, 1912

Lynchailurus pajeros garleppi Matschie, 1912: 259.

HOLOTYPE: ZMB 21244.

TYPE LOCALITY: "von Cuzco in Südost-Peru, im Gebiet des Apurimac, der durch den Ucayali zum oberen Amazonas abwässert."

RANGE: Highland steppes of Peruvian Andes, eastern side.

L. p. pajeros (Desmarest, 1816)

Felis pajeros Desmarest, 1816: 114.

Felis pageros Lesson, 1827: 195.

Felis pampa Schinz, 1831: 164.

Pajeros pampanus Gray, 1867: 269.

Felis passerum Sclater, 1871: 700.

HOLOTYPE: Not designated.

TYPE LOCALITY: "Pampas de Buenos Ayres entre los 35 y 36 grados," Argentina.

RANGE: La Pampa province, central Argentina.

L. p. steinbachi Pocock, 1941

Lynchailurus pajeros steinbachi Pocock, 1941: 264.

HOLOTYPE: BM 34.9.2.31.

TYPE LOCALITY: "Tiraque, Cochabamba, western Bolivia, 4000 m."

RANGE: Highland steppes of Bolivian Andes, eastern slope.

L. p. thomasi (Lönnberg, 1913)

Felis pajeros thomasi Lönnberg, 1913: 7.

HOLOTYPE: Unknown.

TYPE LOCALITY: "Near Quito," Ecuador.

RANGE: Highland steppes of Ecuadorean Andes, eastern side.

Lynchailurus braccatus
(Cope, 1889)

L. b. braccatus (Cope, 1889)

Felis braccata Cope, 1889: 144.

HOLOTYPE: AMNH 354.

TYPE LOCALITY: "Chapada, Matto Grosso," Brazil.

RANGE: Southwestern Brazil (Mato Grosso and Mato Grosso do Sul), Paraguay.

L. b. munoai (Ximenez, 1961)

Felis colocola munoai Ximénez, 1961: 3.

Felis colocola munoai Ximénez, 1970: 1-4.

HOLOTYPE: MHNM 884.

TYPE LOCALITY: "Arroyo Perdido, Departamento de Soriano," Uruguay.

RANGE: Southern Brazil (Rio Grande do Sul), Uruguay.

Specific names applied to unidentifiable specimens: *Felis lineata* Swainson, 1838, and *Felis strigilata* Wagner, 1841, which were applied to Hamilton Smith's (*in* Griffith et al., 1827) drawing.

A name associated with this group that should be excluded is *Lynchailurus pajeros hyperthrix* Schwangart, 1941. This taxon was described based on a misidentified skin of manul (Weigel, 1961).

CONSERVATION

This species group is one of the least well known of the South American cats. They are included in Appendix II of CITES, under the common specific term *Felis colocolo*. The recognition of three species in this group means that their individual ranges are smaller than formerly perceived. An evaluation of the status of these three species is warranted. *Lynchailurus colocolo*, as now restricted, could be the most endangered, because its range is significantly smaller.

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APPENDIX 1 Material Studied

Lynchailurus braccatus

Brazil: AMNH 133977 (skull and skin), AMNH 354 (skull and skin) holotype of *braccata*, FMNH 28335 (skull and skin), USNM 256127 (skull and skin).

Paraguay: AMNH 243110 (skull and skin), AMNH 148573 (skin).

Uruguay: AMNH 189394 (skull and skin).

Lynchailurus colocolo

Central Chile: BM 1.12.27.1 (skull and skin), BM 1.11.18.1 (skull), BM 8.4.13.1 (skull and skin), BM 1.9.25.1 (skull and skin), BM 1.11.6.2 (skull and skin) holotype of *huina*, FMNH 24418 (skull), FMNH 24370 (skull), FMNH 25145 (skin), FMNH 49931 (skin), USNM 391852 (skin).

Northern Chile: FMNH 24358 (skull and skin), USNM 391853 (skull and skin) holotype of *wolff-sohni*.

Chile: BM 43.10.28.3 (skull and skin), BM 1846.11.3.11 (skull), BM 1873.12.16.1 (skull and skin), BM 48.6.26.8 (skull).

Lynchailurus pajeros

Argentina: AMNH 36934 (skin), AMNH 16695 (skull and skin), BM 42.57 (skull), BM 3.11.5.6 (skull and skin), BM 3.2.24.1 (skull and skin), BM 1899.2.22.3 (skull and skin), BM 3.11.5.7 (skull and skin), BM 21.6.7.5 (skull), BM 55.12.24.261 (skull and skin) holotype of *crucina*, BM 34.11.4.5 (skull and skin) holotype of *budini*, BM 3.2.24.1 (skin), BM 84.7 (skin), FMNH 21677 (skin), FMNH 21679 (skin), MACN 16489 (skull), MACN 17816 (skull), MACN 15582 (skull and skin), MACN 14086 (skull and skin), MACN 50446 (skull and skin), MACN 30103 (skull and skin), MACN 1.23 (skin), MACN 29.765 (skin), MACN 25.33 (skin), MACN 34.326 (skin), MACN 34.565 (skin), MACN 34.631 (skin), MACN 34.632 (skin), MACN 37.39 (skin), MACN 37.40 (skin), MACN 37.117 (skin), MACN 39.721 (skin), MACN 41.163 (skin), MACN 49.169 (skin),

MACN 50.456 (skin), MACN 50.457 (skin), MACN 51.164 (skin), MACN 51.167 (skin), MACN 17.821 (skin), MACN 36.230 (skin) holotype of *crespoi*, MACN 34.322 (skin), MCZ 19224 (skull and skin), MCZ 19501 (skull and skin), MCZ 19225 (skin), USNM 171952 (skin), USNM 172786 (skull), USNM 172785 (skull).

Bolivia: BM 34.9.2.31 (skull and skin) holotype of *steinbachi*, EBD 8366 (skin), EBD 8741 (skull), EBD 14430 (skull).

Ecuador: AMNH 76150 (skull and skin), BM 24.4.18.5 (skull and skin) topotype of *thomasi*, FMNH 43291 (skull and skin).

Peru: BM 27.11.1.66 (skull and skin), BM 27.11.1.67 (skull and skin), BM 26.5.3.6 (skin), FMNH 52488 (skull), FMNH 68318 (skull and skin), FMNH 25350 (skin), FMNH 49735 (skin), MVZ 139613 (skull), MVZ 114942 (skull and skin), MVZ 114777 (skull and skin), MVZ 114943 (skull and skin).

South Chile: BM 12.7.12.4 (skull).

APPENDIX 2 Specimens Excluded from the Study

FMNH 104925, Zoo specimen, unknown locality
MACN 4-400, Zoo specimen, unknown locality
MACN 4-45, Unknown locality
MACN 30-8, Zoo specimen, unknown locality
MACN 25.5, Zoo specimen, unknown locality
MACN 26.186, Unknown locality
MACN 26.187, Unknown locality
MACN 50.465, Unknown locality
MACN 50.466, Unknown locality
MACN 15, *O. geoffroy*, Argentina
MVZ 21936, *L. rufus*, Argentina (wrong locality)
MVZ 116007, domestic cat, Peru
MVZ 141633, domestic cat, Peru
UMMZ 125557, *H. yagouaroundi*, Paraguay
UMMZ 125558, *H. yagouaroundi*, Paraguay
USNM 540867, Zoo specimen, unknown locality

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